PHYSIOLOGICAL, ANATOMICAL AND GROWTH RESPONSES OF MANGO
(MANGIFERA INDICA L.) TREES TO FLOODING

By

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In memory of Catherine Munn Fatherson

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Experiments were conducted to determine the effects of soil

flooding on the chemistry of calcareous soils, and on mineral nutrition,

leaf gas exchange, vegetative growth, anatomy, and ethylene evolution of

mango (Mangifera indica L.) trees. Concentrations of NH_4^+, Fe and Mn

were greater, but NO_3^- and P were less, for anaerobically incubated than

for aerobically incubated calcareous soils. To determine the influence

of flooded soil chemical transformations on mineral nutrition and leaf

gas exchange, mango trees were grown with (+Fe) or without (-Fe) iron

fertilizer in calcareous soil, and flooded for 0, 10 or 20 days. Prior

to flooding, leaf gas exchange, total leaf chlorophyll content, and

foliar Mn and Fe concentrations were less for -Fe trees than for +Fe

trees. Chlorophyll, Fe, Mn, and leaf gas exchange increased in flooded

trees relative to nonflooded trees, and this increase was greatest for

the -Fe trees. Flooding reduced vegetative growth and increased the

shoot:root ratio. Rapid and simultaneous reductions in net CO_2 assimilation and stomatal conductance for CO_2 occurred with flooding, yet substomatal CO_2 concentration increased. After floodwaters subsided there was a slow recovery of these physiological variables. The flood-induced decline in leaf gas exchange was not accompanied by reduction in leaf water potential. Hypertrophy of stem lenticels was frequently observed in trees that survived flooding stress, but not in trees that died as a result of flooding. If hypertrophied lenticels were covered to impede gas exchange, the trees died within 2-3 days. Hypertrophy was most rapid at floodwater temperatures of 30° C, but did not occur at 15° C, and was reduced when floodwater dissolved O_2 content was increased to 15 ppm. Lenticel hypertrophy was characterized by a more spherical shape of cells in the phellem and phelloderm, by development of intercellular spaces in the phellem and lenticel filling tissue, and by the production of additional phellem tissue adjacent to the lenticel pore, resulting in a larger pore opening. Ethylene evolution from stem tissue was greater with floodwater dissolved oxygen contents of 1-3 ppm than with O_2 contents of 6-15 ppm. The results of these investigations indicate that although mango is not a hydrophytic plant, it does possess certain adaptations that permit survival under flooded soil conditions.

CHAPTER 1
INTRODUCTION

The mango is one of the world's most widely planted fruit crops
(Anon, 1989a), and is grown in at least 87 countries (Bondad, 1980).
Cultivated for over 4,000 years (Purseglove, 1968), it is an important
food throughout the tropics and an increasingly significant item of
commerce in many tropical, subtropical and temperate areas (Subra, 1981;
Toohill, 1984). In recent years, production of mangos for local and
export markets has led to increased plantings throughout the Caribbean,
Central and South America, Africa, and parts of Australia and North
America (Subra, 1981; Toohill, 1984).

In many regions of the world, mangos are grown in either heavy
soils that impede internal drainage, or in low elevation areas that are
prone to periodic flooding as a result of intense rainstorms. In South
Florida (the major area of commercial mango production in the United
States), high land values have forced new mango plantings into low
elevation areas that are prone to seasonal flooding during the summer
and fall rainy season.

Although numerous studies have been conducted on flooding of fruit
trees (Andersen et al., 1984a, 1984b; Childers and White, 1942; Crane
and Davies, 1985; Davies and Wilcox, 1984; Davies and Flore, 1986a,
1986b, 1986c; Phung and Knipling, 1976; Syvertsen et al., 1983), very
little work has been done to quantify responses of mango to soil
flooding. The small amount of available information regarding mango

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flood tolerance is conflicting, and based almost exclusively on field observations. Some reports indicate that mango trees require good soil drainage for adequate growth and yield (Alfonsi and Brunini, 1980; Popenoe, 1920; Samson, 1986; Valmayor, 1962), whereas others indicate that they are flood tolerant (Chandler, 1958; Jawanda, 1961; Young and Sauls, 1981). Chandler (1958) noted that mangos tolerate shallow, poorly aerated soils, but observed that young mango trees may be injured by poor soil aeration. Mature mango trees appear to tolerate flooding better than young mango trees (Chandler, 1958).

In Florida, the effect of flooding on mangos has been variable. Established mango trees have withstood prolonged periods (months) of flooding, whereas young trees planted in poorly drained areas often die rapidly (K.Mitchell, J.R. Brooks and Son, Inc., personal communication). Flooding of young bearing trees has resulted in tree decline and bloom inhibition (C.Campbell, personal communication). Young and Sauls (1981) reported that mangos on a sandy organic soil withstood flooding for at least 2 months without harm. However, mangos did not perform well under constant poor drainage (Young and Sauls, 1981).

The wide range of plant response to flooding and the conflicting reports of mango flood tolerance indicate the need for definitive studies on this subject. Such studies could assist in the development of sound management programs for mangos in flood-prone areas, and would provide a better basic understanding of fruit tree responses to flooding.

This dissertation includes a literature review of the effects of flooding on soil chemistry, and of plant responses to flooding (Chapter 2). The dissertation also encompasses five separate experiments that

were designed to determine the effects of flooding on: limestone soil chemistry (Chapter 3); mango mineral nutrition (Chapter 4); net gas exchange and vegetative growth of mango (Chapter 5); mango stem lenticel hypertrophy (Chapter 6); and the relationship between floodwater oxygen content, ethylene evolution and mango stem lenticel hypertrophy (Chapter 7). These five experiments were conceived, justified, executed, and written as separate units during a three-year period. As such, there is some redundancy between Chapter 2 (Literature Review) and the introductions for each of Chapters 3 through 7.

CHAPTER 2
LITERATURE REVIEW

Effect of Flooding on Chemical, Physical
and Biological Processes in the Soil

Flooding results in the displacement of O_2 from the soil pores by water and the consumption of available oxygen by obligate and facultatively aerobic organisms. Thus, flooded soils may become nearly devoid of O_2 within a few hours (Ponnamperuma, 1984). The absence of O_2 in flooded soils results in the predominance of facultative and obligate anaerobes that use NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-}, CO_2, N_2, H^+, and various organic molecules as terminal electron acceptors in oxidative phosphorylation and electron transport processes (Ponnamperuma, 1984). After oxygen is consumed in a flooded soil, these constituents are reduced, generally in a sequential manner, to N_2, Mn^{2+}, Fe^{2+}, H_2S, CH_4, NH_4^+ and H_2, respectively (Rowell, 1981). These oxidized soil constituents and their corresponding reduced forms comprise the redox couples of a soil solution.

Redox potential (Eh) is a mixed potential of all the redox couples in a soil solution, and is used to determine the oxidation-reduction status of the soil (Gambrell and Patrick, 1978; Ponnamperuma, 1972, 1984). Typically, Eh of aerobic soil ranges between 300 and 800 mv, and that of anaerobic soil between -450 and 200 mv (Ponnamperuma, 1972). Determination of Eh is most useful in anaerobic soil solutions where the

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high concentrations of redox-active ions and organic molecules, and the high H^+ exchange currents increase the stability of the redox potentials (Bohn, 1971). However, variations among soil microsites in mineral composition (redox couples) and in bacterial or root populations necessitate numerous measurements to ensure accurate assesment of soil Eh (Rowell, 1981). In aerated systems, measurement of Eh is much less useful; metal ions and organic compounds are oxidized and less soluble, reducing the concentration of redox couples and the stability and reproducibility of the measurements (Bohn, 1971).

Soil Eh is influenced by pH (Armstrong, 1975); therefore, measurements are often converted to standard pH values (59 mv per pH unit) (Armstrong, 1975). Redox potential is also influenced by the concentration of the specific redox couples in the soil solution, since high concentrations of a redox couple can result in the buffering (poise) of the Eh at a particular potential (Rowell, 1981). High levels of soil organic matter tend to increase bacterial respiration rates, resulting in a more rapid decrease in Eh (Rowell, 1981). Temperature can also influence Eh by regulating bacterial respiration rates.

After flooding, the pH of an acid soil increases mainly due to iron reduction, whereas the pH of an alkaline soil decreases due to CO_2 accumulation from bacterial respiration (Ponnamperuma, 1972, 1984). Carbon dioxide reacts with water to form carbonic acid (H_2CO_3), which dissociates into H^+ and HCO_3^- ions (Buckman and Brady, 1968). In alkaline soils, H^+ ions neutralize OH^- ions in the soil solution, resulting in acidification of the soil solution. These flood-induced pH changes can increase the exchange capacity of an acid soil, but decrease that of an alkaline soil (Ponnamperuma, 1984).

The decomposition (mineralization) of organic matter proceeds at a much slower rate under anaerobic conditions than in the presence of oxygen, and nitrification ceases, resulting in an increase in NH_4^+ in the soil solution (Ponnamperuma, 1984). In addition to increases in NH_4^+ concentration, flooding often results in an increase in other soil nutrients due to an increase in the amounts of dissolved and suspended nutrients, and solubilization of P, Si, Fe and Mn (Ponnamperuma, 1984). Increases in the ionic strength of the soil solution often result in displacement of K, Ca and Mg from the soil exchange complex, thereby increasing the concentration of these elements in the soil solution (Ponnamperuma, 1984). In porous soils, however, flooding can result in nutrient losses by leaching (Ponnamperuma, 1984), and NO_3^- disappears rapidly from flooded soils by reduction, leaching or denitrification (McGarity, 1961; Ponnamperuma, 1972, 1984; Stefanson and Greenland, 1970). Flooding also results in a reduction in soil temperature, swelling of soil colloids and loss of soil structure, all of which can adversely effect nutrient absorption and availability (Ponnamperuma, 1984).

Flooding and Plant Mineral Nutrition

For many plant species exposed to anaerobic stress, root decay (Stolzy et al., 1975), and reductions in root metabolism (Labanauskas et al., 1971; Trought and Drew, 1980) and root growth (Kozlowski, 1984) often result in decreased plant nutrient concentrations. Although nutrient uptake is generally inhibited, plant nutrient concentrations are dependent on soil conditions as well as plant uptake responses

(Kozlowski and Pallardy, 1984). For example, in soils that are moderately or severely deficient in P, flooding can result in increased P solubility due to flood-induced shifts in soil pH. In such cases, increased P availability may counteract the inhibition in P uptake resulting from reduced root metabolism. Additionally, the reduction of ferric Fe and manganic Mn to more soluble forms often makes these elements more available to plants. Although plant nutrient concentrations may increase with short-term flooding, long-term flooding generally results in decreased concentrations of plant macronutrients, due to degeneration of the root system (Kozlowski and Pallardy, 1984).

For some flood-tolerant species, morphological adaptations to flooding may allow continued uptake of nutrients under flooded conditions. In these plants, initiation of adventitious roots at the surface of the submerged soil or in the floodwater permits continued nutrient uptake in the most oxidized soil environment (Hook et al., 1971; Kozlowski, 1984; Kozlowski and Pallardy, 1984). Additionally, the development of aerenchymatous tissues in the roots and stems of some flood tolerant plants can permit internal oxygen diffusion to the roots, thereby maintaining root metabolic function (Armstrong, 1968; Coutts and Armstrong, 1976). Provided with adequate nutrient availability in flooded soils, flood-tolerant plants are often able to absorb sufficient nutrients for maintaining plant growth. Thus, flooding often results in decreased nutrient absorption in flood-intolerant plants, but increased nutrient absorption in flood-tolerant species (Kozlowski and Pallardy, 1984).

Flooding, Leaf Gas Exchange and Plant Water Status

One of the earliest detected physiological responses of fruit trees to flooding is a reduction in stomatal conductance (g_s) (Andersen et al., 1984a, 1984b; Crane and Davies, 1989; Davies and Flore, 1986a, 1986b, 1986c; Pereira and Kozlowski, 1977; Schaffer and Ploetz, 1989; Schaffer et al., 1991; Smith and Ager, 1988; Syvertsen et al., 1983). Although many woody plants exhibit a decrease in g_s within 1 to 3 days after flooding (Andersen et al., 1984a; Crane and Davies, 1989), the duration of flooding required for decreases in g_s can vary among species. For example, g_s of Citrus aurantium and Citrus jambhiri seedlings decreased 4 and 8 days after flooding, respectively (Syvertsen et al., 1983). Seasonal effects of flooding on g_s have also been observed. In general, flooding during the spring or summer results in more rapid reductions in g_s than flooding in the fall (Andersen et al., 1984b; Olien, 1987).

Flood-induced decreases in g_s result in reduced transpiration (E) for a number of woody plant species (Crane and Davies, 1989; Davies and Flore, 1986b; Kozlowski and Pallardy, 1984; Olien, 1989; Phung and Knipling, 1976; Ploetz and Schaffer, 1987; Regehr et al., 1975; Sena Gomes and Kozlowski, 1980; Smith and Ager, 1988; Sojka and Stolzy, 1980). For many species, reductions in g_s are transitory, and g_s usually increases to that of nonflooded plants after the flooding stress is relieved (Crane and Davies, 1988; Davies and Flore, 1986b; Joyner and Schaffer, 1990; Schaffer et al., 1991; Smith and Ager, 1988). However, for some species exposed to prolonged flooding, g_s does not recover, or

recovers very slowly after plants are removed from flooding (Davies and Flore, 1986b; Schaffer et al., 1991; Smith and Ager, 1988).

Various hypotheses have been suggested to account for reductions in stomatal aperture under flooded conditions. In some studies, flood-induced stomatal closure has been attributed to a reduction in leaf water potential resulting from decreased water uptake by the roots (Heincke, 1932; Kozlowski and Pallardy, 1984; Kramer, 1954) or reductions in root hydraulic conductivity (Jackson et al., 1978; Kramer, 1952; Syvertsen et al., 1983; Willey, 1970), possibly as a result of decreased cell membrane permeability (Bradford and Yang, 1981; Bradford and Hsiao, 1982; Kramer, 1969; Slatyer, 1967). Under anaerobic conditions, decreases in ATP and respiratory substrates, production of toxic anaerobic respiration byproducts (i.e., acetaldehyde and ethanol) in the plant, and production of toxic compounds in the soil may affect membrane integrity and function (Drew, 1983). Andersen et al. (1984b) attributed decreased conductance to water flow in roots and stems to plugging of xylem vessels.

For most plants, early stomatal closure due to flooding occurs without any reduction in plant water status (Andersen et al., 1984a; Bradford and Hsiao, 1982; Davies and Wilcox, 1984; Davies and Flore, 1986a, 1986b, 1986c; Jackson and Hall, 1987; Pereira and Kozlowski, 1977; Smith and Ager, 1988). Reductions in root or stem hydraulic conductivity (Andersen et al., 1984a; Davies and Wilcox, 1984; Davies and Flore, 1986b; Syvertsen et al., 1983), reductions in K ion concentration (Stolzy et al., 1975; Peaslee and Moss, 1966; Letey et al., 1961a, 1961b), or hormonal factors (El-Betalgy and Hall, 1974; Hiron and Wright, 1973; Reid and Bradford, 1984; Reid and Crozier, 1971;

Reid et al., 1969; Wright and Hiron, 1969) have been postulated to cause flood-induced stomatal closure in the absence of a reduction in plant water status. Reid and Bradford (1984) suggested that reduced cytokinin and/or gibberellin synthesis in flooded roots, possibly in combination with increased ABA levels, may be responsible for anoxia-induced stomatal closure. Davies and Flore (1985) observed a reduction in g_s when root exudate from flooded blueberry plants was applied to nonflooded plants, suggesting the presence of a translocatable substance originating in the roots. Schaffer and Ploetz (1991), working with approach-grafted avocado trees, also reported the presence of a translocatable substance involved in stomatal regulation. However, no universal mechanism for stomatal regulation in flooded plants has been demonstrated.

The hypothesis that flood-induced stomatal closure limits net CO_2 assimilation (A) is supported by studies in which g_s, A and the internal partial pressure of CO_2 decreased simultaneously in flooded plants (Davies and Flore, 1986a, 1986c). However, non-stomatal inhibition of A also has been reported with flooding (Beckman et al., 1987; Bradford, 1983; Childers and White, 1942; Moldau, 1973). It has been postulated that for g_s to regulate A, reductions in stomatal aperture must occur prior to reductions in A. In some flooding studies, however, A and g_s decrease simultaneously (Ploetz and Schaffer, 1989; Schaffer and Ploetz, 1989; Smith and Ager, 1988). Increases in internal partial pressure of CO_2 observed concomitant with decreases in A and g_s (Schaffer and Ploetz, 1989), suggest that, for some plants, flooding inhibits A more than g_s (Farquhar and Sharkey, 1982).

For blueberry, where stomatal closure appears to be regulating A during the early stages of a flooding cycle, long-term flooding eventually results in decreased carboxylation efficiency (Davies and Flore, 1986b), thereby indicating a direct effect of flooding on the photosynthetic apparatus. Decreased mesophyll conductance may be due to reduced chlorophyll content or changes in carboxylation enzymes (Kozlowski, 1982; Vu and Yelenosky, 1991), or to feedback inhibition due to starch accumulation (Wample and Thornton, 1984). Beckman et al. (1987) reported the occurrence of a translocatable photosynthetic inhibitor in the xylem sap of flooded cherry trees. Application of flooded tree xylem sap exudate to nonflooded trees resulted in a rapid decrease in A, although g_s was unaffected. With nonstomatal limitations to CO_2 assimilation, changes in A may regulate g_s, since stomata function to maintain a constant substomatal CO_2 partial pressure (Wong et al., 1979).

Stomatal and nonstomatal limitations to A resulting from flooding may be species-dependent. The simultaneous decreases in A and g_s often observed in flooded plants (Davies and Flore, 1986c; Ploetz and Schaffer, 1989; Schaffer and Ploetz, 1989; Smith and Ager, 1988) suggest independent regulation of these two physiological processes.

Flooding and Plant Ethylene Evolution

Although ethylene is often produced in flooded soils (Crane and Davies, 1986; Smith and Russell, 1969; Smith and Dowdell, 1974), and may be an environmental source of ethylene in flooded plants, increased ethylene synthesis has been observed in plants exposed to flooded soil

conditions (Bradford, 1981; El-Beltagy and Hall, 1974; Jackson and Campbell, 1975, 1976; Kawase, 1972, 1976). Ethylene can induce many of the symptoms commonly associated with plant flooding stress, such as leaf epinasty (Bradford and Yang, 1980a; Jackson and Campbell, 1975, 1979), leaf senescence (El-Betalgy and Hall, 1974), adventitious rooting (Drew et al., 1979; Kawase, 1971), aerenchyma development (Drew et al., 1979, 1981), and stem and lenticel hypertrophy (Kozlowski, 1984; Reid and Bradford, 1984). Anaerobiosis stimulates the production of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) in the roots of flooded tomato plants. However, anaerobiosis inhibits the production of ethylene by the roots, since conversion of ACC to ethylene is oxygen-dependent. The ACC moves in the transpiration stream, resulting in increased ethylene synthesis in the shoots (Bradford and Yang, 1980a, 1980b). The biosynthetic pathway of ethylene, from methionine to S-adenosylmethionine (SAM) to ACC, has been well-documented for tomato plants (Yang, 1980; Yang et al., 1982). However, alternative precursors and pathways may exist in other plant species (Jackson, 1985).

Other plant hormones may interact with ethylene or influence the production of ethylene or ethylene precursors under flooded conditions. Elevated auxin levels have been observed in the shoots of flooded plants (Phillips, 1965; Wample and Reid, 1979), presumably due to reductions in auxin transport or metabolism (Phillips, 1964; Reid and Bradford, 1984), and increased auxin levels have been shown to stimulate ethylene production (Abeles and Rubenstein, 1964; Yu and Yang, 1979). Although cytokinins promote ACC and ethylene synthesis (Reid and Bradford, 1984), levels of cytokinins have been shown to decrease in flooded plants

(Burrows and Carr, 1969). In contrast, flooding stress can promote ABA production (Hall et al., 1977; Wright and Hiron, 1972), and ABA inhibits ACC and ethylene synthesis (Reid and Bradford, 1984).

Flooding and Plant Growth

In certain plants, rapid stomatal closure maintains turgor and may permit continued growth under flooded conditions (Regehr et al., 1975). However, flood-induced inhibition of plant growth occurs in many species (Andersen et al., 1984a; Davies and Wilcox, 1984; Kozlowski, 1984; Tang and Kozlowski, 1982; Yu et al., 1969), partly due to stomatal closure and reduced CO_2 assimilation (Phung and Knipling, 1976; Regehr et al., 1975; Stolzy et al., 1964). In general, for most flood-intolerant species, flooding adversely affects root growth and viability due to root necrosis and pathogen infection (Kozlowski, 1984; Stolzy and Sojka, 1984). Flooding also curtails shoot elongation, and reduces leaf area by reducing leaf initiation and leaf expansion, and by hastening leaf senescence (Kozlowski, 1984). Root growth and survival is generally more affected by flooding than is shoot growth, resulting in a reduced root-to-shoot ratio (Kozlowski, 1984).

Influence of Flooding on Plant Morphology and Anatomy

Many plants adapt to flooded conditions by formation of adventitious roots or enlarged lenticels that enhance internal oxygen diffusion to the roots (Andersen et al., 1984a; Coutts, 1982; Hook and Scholtens, 1978; Kozlowski, 1984; Kramer, 1983; Pereira and Kozlowski,

1977; Philipson and Coutts, 1978), or function as excretory organs for the elimination of potentially toxic plant metabolites (Chirkova and Gutman, 1972). Wetland plants often have greater root porosities due to the separation and configuration of cortical cells, and exhibit greater tissue porosity and aerenchyma development than mesophytic species (Justin and Armstrong, 1987). Jensen et al. (1969) reported that decreased soil oxygen and increased light and temperature were associated with greater root porosities. Yu et al. (1969) found increased root porosities in some plants subjected to flooding. In wetland plants, internal oxygen transport to roots is often adequate for root respiration (Barber et al., 1962; Conway, 1937; Teal and Kanwisher, 1966) as well as for diffusion into, and aeration of, anaerobic rooting media (Armstrong, 1964, 1967, 1968, 1978; Hook et al., 1970, 1972).

Kozlowski (1984) observed that older trees generally tolerate flooding better than seedlings or saplings. Older woody roots are more tolerant of flooding than non-woody roots (Coutts, 1982; Coutts and Philipson, 1978), probably due to the higher growth rates, respiration rates and oxygen requirements of younger root tissues (Lahde, 1966; Luxmore and Stolzy, 1972). This may partly explain why younger trees, with proportionally more young root tissues, are sometimes more sensitive to flooding than older trees.

CHAPTER 3
FLOOD-INDUCED CHEMICAL TRANSFORMATIONS IN CALCAREOUS
AGRICULTURAL SOILS OF SOUTH FLORIDA

Introduction

Tropical fruit crops in Florida have an annual farm gate value of
over $40 million (Anon, 1987). These crops traditionally have been
grown on soils of the Krome very gravelly loam series (loamy-skeletal,
carbonatic, hyperthermic Lithic Rendoll) (Anon, 1989b; Burns et al.,
1965; Leighty and Henderson, 1958). This soil has a pH of 7.2 to 7.6,
and is excessively well-drained due to the porous limestone parent
material that is usually present at 18 cm or less below the soil
surface. Krome series soils occur in sites at elevations ranging from
2.4 to 4.3 m above sea level and may be even lower in some areas.
Although normally well-drained, low lying areas of this soil type are
prone to flooding during periods of high rainfall.

In recent years, urbanization has forced tropical fruit crop
production in Florida into areas characterized by the Chekika very
gravelly loam soil series (loamy-skeletal, carbonatic, hyperthermic
Lithic Udorthent) (Anon, 1989b; Leighty and Henderson, 1958). This soil
is derived from the same limestone parent material as the Krome soil but
has less soil development. The soil reaction and physical
characteristics of this soil are similar to, but more variable than,
those of the Krome soil series. Due to low elevation and shallow depth

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to the water table, Chekika soils are subject to annual flooding in most years. The high pH of both soils makes minor element nutrition of many crops problematic and can be a major production cost (Davenport, 1983; Malo, 1966; Schaffer et al., 1988).

Chemical transformations that occur in flooded soils have been documented for several soil types (Armstrong, 1975; Gambrell and Patrick, 1978; Gotoh and Patrick, 1972, 1974; Mahapatra and Patrick, 1969; Patrick and Mahapatra, 1968; Ponnamperuma, 1972, 1984; Reddy and Patrick, 1983; Shapiro, 1958). However, flood-induced chemical changes have not been documented for soils primarily composed of only slightly altered limestone. This information is necessary for the development of crop management practices which maximize production efficiency of perennial crops grown on flood-prone limestone soils. The objective of this study was to determine the chemical transformations that occur in Krome and Chekika very gravelly loam soils in response to flooding.

Materials and Methods

Soils

Krome very gravelly loam soil was obtained from a sodded orchard site with a long history of fruit tree cultivation. Chekika very gravelly loam soil was obtained from a virgin tract of land. Both sites had been recently plowed, but the Chekika site had never been cropped or amended with fertilizers. Thus, both soil samples contained large amounts of plant residues which had been incorporated during plowing. Plant residue incorporation resulted in C:N ratios (w/w) of 13.9% : 0.58% (24:1) and 11.0% : 0.39% (28:1) for the Chekika and Krome soil

samples, respectively. The soil samples were air-dried at ambient (22-34°C) temperatures and passed through a 1.0-mm sieve.

Soil Redox Potential and pH

Soil redox potential (Eh) and pH of flooded Krome and Chekika soils were monitored over a 35-day period. Three 200 g samples of each soil were incubated in the dark at 22°C in 0.47-L containers with sufficient deionized H_2O to create a 3.8 cm water column above the soil. The containers were covered with Parafilm to prevent evaporation of the water. Redox potential was determined using a calomel reference electrode and three platinum-tip microelectrodes, as described by Stolzy and Letey (1964). The microelectrode platinum tip was fused to a heavy gauge brass alloy rod and the junction sealed in an epoxy resin (Bohn, 1971; Ponnamperuma, 1972). The microelectrodes were placed in the soil to a depth of approximately 7 cm and measurements were recorded when a stable millivolt reading was reached, usually within 5 min. The reading was adjusted by the addition of +245 mv to compensate for the potential of the reference electrode. Redox potential was monitored daily during the first week of submergence, at about 4-day intervals during the 2nd and 3rd weeks, and at about weekly intervals thereafter. Concurrent with Eh determinations, soil pH was monitored with a pH meter.

Chemical transformation studies

For each soil type, 25-g soil samples were placed in 160-ml serum bottles. Samples were either aerobically incubated (nonflooded) at field capacity moisture content (4 ml water/25 g soil), or anaerobically incubated (flooded) in 50 ml water. For the flooded treatment, after

water was added, serum bottles were sealed with rubber septae and purged
three times with nitrogen gas to ensure anaerobiosis. Serum bottles
were incubated in the dark at $22^{\circ}C$ in covered trays with 1 cm of water
in the bottom to prevent the aerobic treatments from drying out. After
0, 1, 3, 5 and 7 weeks of incubation, 12 samples of each soil type, six
from each incubation treatment, were subjected to extraction with a
neutral 1N NH_4OAc solution for determining concentrations of extractable
K, Fe, Mn, Mg and Ca (Thomas, 1982). Simultaneously, 12 additional
samples of each soil type, six from each incubation treatment, were
subjected to extraction with a 2N KCl solution for determining
concentrations of NH_4^+, NO_3^- and P. Phosphorus concentrations were
determined after 0, 1, 3 and 7 weeks of incubation, but not after week
5. Thus, for all elements or compounds (with the exception of P), there
was a factorial arrangement of treatments (2 soils x 2 incubation
treatments x 5 extraction dates) that was replicated six times in a
completely randomized design. For the flooded treatments, a
proportionally smaller amount of extracting solution of greater
concentration was used to compensate for the dilution effect of the
floodwater. Concentrations of extractable K, Fe, Mn, Mg and Ca were
determined by flame atomic absorption spectrometry (Baker and Suhr,
1982) (Atomic Absorption Spectrophotometer Model 2380, Perkins-Elmer
Corp., Norwalk, CT). Concentrations of extractable NH_4^+ and NO_3^- were
determined colorimetrically using an autoanalyzer (Technicon
Autoanalyzer II, Technicon Instruments Corp., Tarrytown, NY) and
extractable P concentration was determined colorimetrically using a
recording spectrophotometer (Shimadzu Recording Spectrophotometer Model
UV-160, Shimadzu Scientific Instruments, Inc., Norcross, GA) (Anon,

1979). Data were analyzed by analysis of variance and linear and nonlinear regression (SAS Institute, 1985).

Results and Discussion

Soil Redox Potential and pH

Immediately after flooding, Eh of both soils was +300 mv (Fig. 3-1A). Redox potential declined sharply to a minumum potential during the first few days of flooding, then increased to a post-flood maximum before finally decreasing to a stable potential, a pattern typical of flooded soils (Ponnamperuma, 1972). Final Eh for both soils was -165 mv. The greater initial decrease in Eh for the Chekika than for the Krome soil may have been due to the lower initial concentration of redox system components in the Chekika soil; specifically, lower concentrations of extractable NO_3^-, Mn and Fe (Figs. 3-2, 3-3) (Ponnamperuma, 1972). These nutrients can buffer the redox system by serving as electron acceptors under anaerobiosis (Patrick and Mahapatra, 1968). The greater concentration of redox system components in the Krome soil apparently poised the redox system, preventing the Eh from becoming as negative as the less fertile Chekika soil. For both soils, Eh stabilization by day 21 indicated a reduced respiration rate, possibly due to depletion of readily oxidizable organic matter, depletion of electron acceptors, and the stabilizing effect of the mobilized iron and manganese (Rowell, 1981).

Prior to incubation, pH was 7.9 for the Chekika soil and 7.5 for the Krome soil (Fig. 3-1B). In general, the pH of both soils gradually decreased until a stable pH of about 7.25 was reached on day 21. Soil

pH decreased with flooding since the carbonate system predominates over the redox system in alkaline soils (Ponnamperuma, 1972). Bacterial respiration leads to CO_2 accumulation (Ponnamperuma, 1972; Russell, 1977), and consequent H_2CO_3 formation (Buckman and Brady, 1968). In alkaline soils the dissociation of H_2CO_3 into H^+ and HCO_3^- results in acidification of the soil solution.

Chemical Transformation Studies

Ammonium nitrogen. Prior to incubation, concentrations of KCl-extractable NH_4^+ were similar for both soils (Fig. 3-2). With time, flooded soils developed higher NH_4^+ concentrations than nonflooded soils throughout the experiment. Regardless of soil type, NH_4^+ generally increased with flooding until week 5 and then slightly decreased. Maximum concentrations were greatest for the Krome soil. Anaerobiosis curtails microbial oxidation of NH_4^+ to NO_3^- (Patrick and Mahapatra, 1968; Ponnamperuma, 1972; Reddy and Patrick, 1983) but mineralization of organic N to NH_4^+ continues, resulting in increased NH_4^+ concentrations. For the nonflooded treatments, NH_4^+ of the Krome soil slightly decreased over the course of the study, but increased for the Chekika soil up to week 5 before decreasing at week 7.

Nitrate nitrogen. Prior to incubation, concentrations of KCl-extractable NO_3^- were greater for the Krome soil (23.4 $\mu g/g$ soil) than for the Chekika soil (4.2 $\mu g/g$ soil) (Fig. 3-2). For both soils, NO_3^- decreased to nearly 0 ppm after one week of flooding. Nitrate reduction occurs rapidly in anaerobic soils (Patrick and Mahapatra, 1968; Reddy and Patrick, 1983) due to the presence of facultative organisms that transform NO_3^- to N-containing gases at low oxygen tensions

(Ponnamperuma, 1972). Denitrification occurs quickly because NO_3^- is the first redox constituent to disappear from the soil following O_2 depletion (Reddy and Patrick, 1983). For nonflooded soils, NO_3^- content generally increased over the course of the experiment, presumably due to mineralization of organic matter and subsequent nitrification.

Manganese. Prior to incubation, concentrations of NH_4OAc-extractable Mn were approximately three times greater for the Krome soil than for the Chekika soil (Fig. 3-3). For both soils, flooding resulted in a steady increase in extractable Mn over time. With flooding, maximum Mn concentrations were approximately 40 and 7 times greater than the initial Mn concentrations of the Krome and Chekika soils, respectively. The increase in extractable Mn with anaerobic incubation is consistent with results of other studies that indicate an increase in soluble Mn with flooding (Ponnamperuma, 1972). After NO_3^-, MnO_2 is the next redox system component likely to be reduced in an anaerobic soil. Possibly because of the relatively low NO_3^- levels in the experimental soils, large amounts of Mn became more extractable in both soils during the first 7 days of flooding. Biological reduction of Mn^{4+} in MnO_2 and an increase in the concentration of water-soluble Mn^{2+} are two of the principal transformations of Mn in flooded soils. For both nonflooded soils, there was a gradual decrease in extractable Mn over the course of the study.

Iron. Prior to incubation, concentrations of NH_4OAc-extractable Fe were similar for both soils (Fig. 3-3). For both soils, there was a large increase in extractable Fe after one week of flooding, and maximum Fe concentrations (week 5) were approximately 30 and 15 times greater than the initial concentrations for the Krome and Chekika soils,

respectively. For both soils, aerobic incubation resulted in linear increases in extractable Fe over time, but such increases were less than with anaerobic incubation. Under anaerobiosis, the Fe^{3+} - Fe^{2+} redox couple is the next constituent of the redox system likely to be reduced after Mn (Ponnamperuma, 1972). However, reduction of redox system components does not always occur sequentially; often one redox component is not completely reduced before the next most easily reduced component begins to be reduced (Patrick and Mahapatra, 1968). The reduction of Fe and its increased solubility is often one of the most important chemical changes to occur in flooded soils (Ponnamperuma, 1972), and the increase in extractable Fe observed in the present study is consistent with this observation.

Magnesium, potassium, calcium and phosphorus. Prior to incubation, concentrations of NH_4OAc-extractable Mg were greater for the Krome soil than the Chekika soil (50 and 30 $\mu g/g$ soil, respectively (Fig. 3-4). The concentration of Mg increased linearly with time in both soil types, but the rates of increase were greater for the flooded treatments.

Prior to incubation, concentrations of NH_4OAc-extractable K were greater for the Krome than for the Chekika soil (50 and 35 $\mu g/g$ soil, respectively (Fig. 3-4). In general, for both soils, K increased over time regardless of incubation treatment.

Although there was no direct evidence for the presence of $CaCO_3$ in the experimental soils, levels of $CaCO_3$ are presumably high since these soils are derived from limestone ($CaCO_3$) parent material. At day 0, the concentration of NH_4OAc-extractable Ca was greater for the Krome soil (4.1 mg/g) than for the Chekika soil (3.2 mg/g) (Fig. 3-5). For both

soils, extractable Ca of flooded and nonflooded treatments generally increased over the course of the experiment. However, the rate of increase was greater for the nonflooded treatments. For both soils, a test for homogeneity of the slopes of the regression lines for Ca concentration in Fig. 3-5 showed that while the y intercept was identical for flooded and nonflooded treatments, there was a significant difference in the slopes of the lines ($P < 0.01$).

Prior to incubation, KCl-extractable P concentrations were more than three times greater for the Krome soil (1.95 µg/g soil) than for the Chekika soil (0.64 µg/g soil) (Fig. 3-5). For both soils, flooding and nonflooding resulted in decreases in P, but the rate of decline was more rapid for the anaerobic treatments.

With flooding, increased mobilization of NH_4^+, Fe^{2+} and Mn^{2+} results in an increase in the ionic strength of the soil solution (Reddy and Patrick, 1983). Mobilization of relatively large amounts of these reduced cations can displace Mg^{2+}, Ca^{2+} and K^+ from the exchange complex, resulting in increased levels of these cations in the soil solution. Such enhancement of elemental solubility with flooding is consistent with the changes in elemental extractability observed in the present study. For example, although extractable Mg increased in both soils regardless of incubation treatment, increases were greatest when soils were flooded. Although the presence of $MgCO_3$ was not determined for soils of the present study, in flooded alkaline soils dissolution of $MgCO_3$ and the increased concentration of reduced cations in the soil solution can lead to displacement of Mg^{2+} from the exchange complex, thereby increasing its concentration in the soil solution.

Similarly, although there was no significant difference between flooded and nonflooded treatments in extractable K, the trend toward slightly higher extractable K concentrations in the flooded soils may be due to displacement of K^+ from the exchange complex by the increased concentration of reduced cations in the flooded soil solution (Reddy and Patrick, 1983).

Although concentrations of extractable Ca at week 7 were greatest for the nonflooded treatments, there was a greater amount of extractable Ca in the flooded treatments during the first 2 weeks of the experiment (Fig 3-5). Displacement of Ca^{2+} from the exchange sites may account in part for the reduction in extractable P in the anaerobic treatments at that time (Fig. 3-5), because Ca^{2+} and P can react to form insoluble calcium phosphate compounds. For most flooded soils, soluble P tends to increase under flooded conditions (Patrick and Mahapatra, 1968; Shapiro, 1958), mainly due to the reduction of iron phosphate compounds (Reddy and Patrick, 1983; Patrick and Mahapatra, 1968). In alkaline soils, however, P does not usually increase because soluble P is controlled by the calcium system (Reddy and Patrick, 1983). The decrease in extractable P in nonflooded treatments prior to week 5 may be due to microbial P metabolism, or the dissolution and subsequent precipitation of Ca and P that occurred during collection, air-drying and subsequent incubation of the samples at field capacity moisture content.

Conclusions

Despite relatively low native fertility, significant chemical transformations occur in Krome and Chekika very gravelly loam soils

subjected to flooding. The increases in extractable Mn, Fe and Mg in both flooded soils is consistent with increased elemental solubility reported in other flooding studies. This increased solubility could exacerbate leaching losses or result in nutrient toxicities, although in the present study concentrations of extractable elements do not appear to reach phytotoxic levels. Additional studies are needed to determine if flooding can increase the assimilation of elements such as Fe and Mn without harmful effects to the crop. In some mango growing areas, such as South Florida, the ability exists to regulate flooding duration and floodwater depth in flood-prone agricultural areas. Therefore, annual flooding cycles should be evaluated for their potential to alleviate minor element deficiencies in crops grown on these limestone soils.

Fig. 3-1. Effect of flooding on soil redox potential and pH of Krome and Chekika very gravelly loam soils during a 35-day flooding period. A) Redox potential (Eh). B) pH. For both figures, symbols represent means of three soil samples ± SE. Where not shown, for both figures, SE bars are within the area of the symbol.
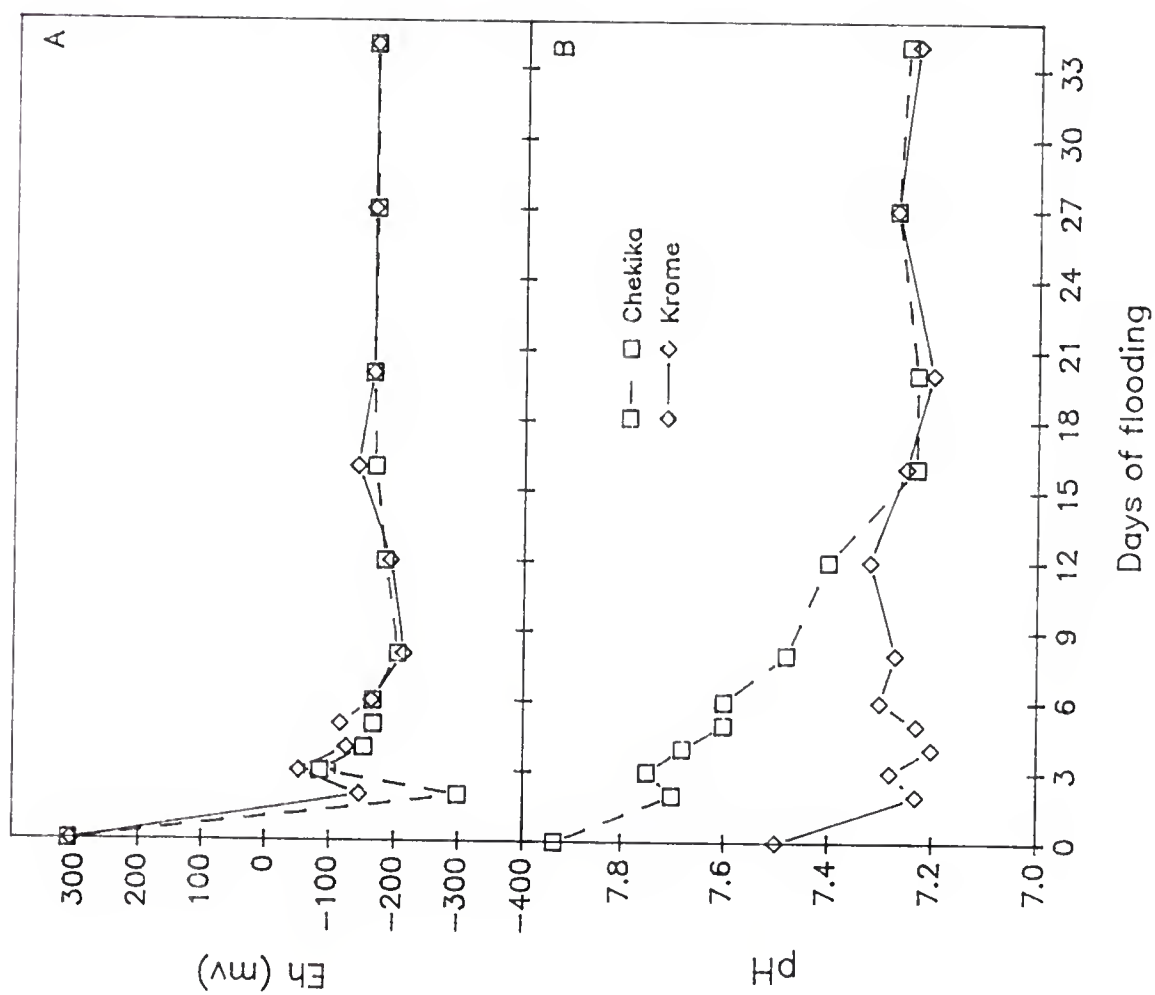
Fig. 3-2. Concentrations of 2N KCl-extractable NH$_4^+$ and NO$_3^-$ in flooded and nonflooded Krome and Chekika very gravelly loam soils. Each symbol represents one replication.

Chekika

μg NH₄⁺/g soil

O——O nonflooded
$y = 7.8 - 8.2x + 5.8x^2 - 0.7x^3$
$r^2 = 0.90$

Δ---Δ flooded
$y = 12.6 - 8.0x + 9.2x^2 - 1.0x^3$
$r^2 = 0.82$

μg NO₃⁻/g soil

O——O nonflooded $y = 2.66 + 4.99x$ $r^2 = .93$

Δ---Δ flooded

Krome

O——O nonflooded
Δ---Δ flooded
$y = 6.5 + 39.6x - 3.6x^2$
$r^2 = 0.94$

O——O nonflooded
$y = 21.2 - 33.9x - 8.24x^2 + 0.6x^3$; $r^2 = 0.90$

Δ---Δ flooded

Time (weeks)

Fig. 3-3. Concentrations of $1N$ NH_4OAc-extractable Mn and Fe in flooded and nonflooded Krome and Chekika very gravelly loam soils. Each symbol represents one replication.

Fig. 3-4. Concentrations of $1N$ NH_4OAc-extractable Mg and K in flooded and nonflooded Krome and Chekika very gravelly loam soils. Each symbol represents one replication.

Chekika

μg Mg / g soil

O——O nonflooded   y = 25.3 + 6.1x;   r² = 0.73
Δ - - Δ flooded   y = 24.5 + 10.1x;   r² = 0.90

μg K / g soil

O——O nonflooded   y = 33.8 + 3.7x;   r² = 0.91
Δ - - Δ flooded   y = 26.6 + 7.8x;   r² = 0.95

Time (weeks)

Krome

O——O nonflooded   y = 45.6 + 9.0x;   r² = 0.79
Δ - - Δ flooded   y = 46.0 + 14.7x;   r² = 0.88

μg Mg / g soil

O——O nonflooded   y = 41.6 + 9.9x;   r² = 0.95
Δ - - Δ flooded   y = 45.4 + 9.9x;   r² = 0.91

μg K / g soil

Time (weeks)

Fig. 3-5. Concentrations of 1N NH$_4$OAc-extractable Ca and 2N KCl-extractable P in flooded and nonflooded Krome and Chekika very gravelly soils. Each symbol represents one replication.

CHAPTER 4
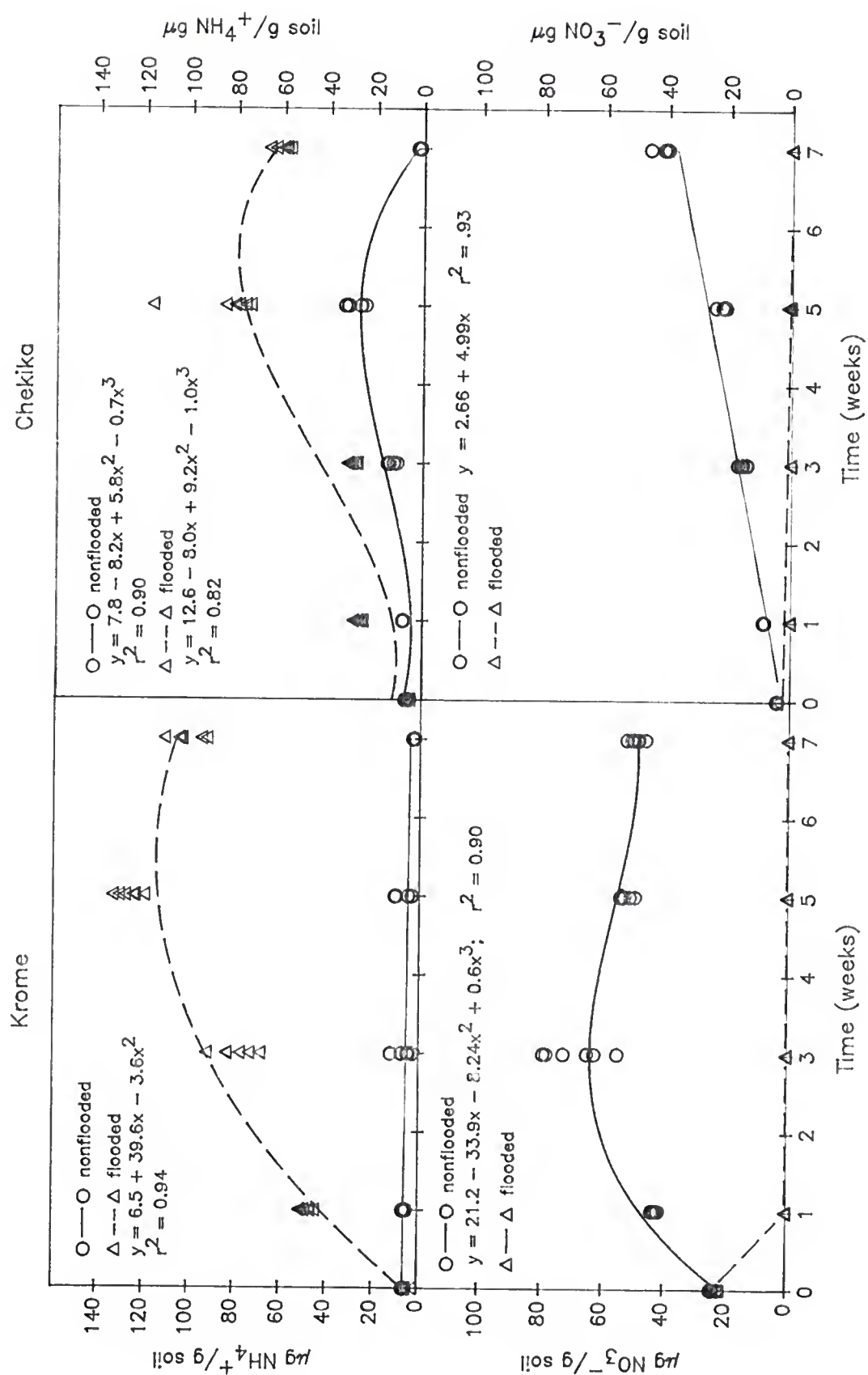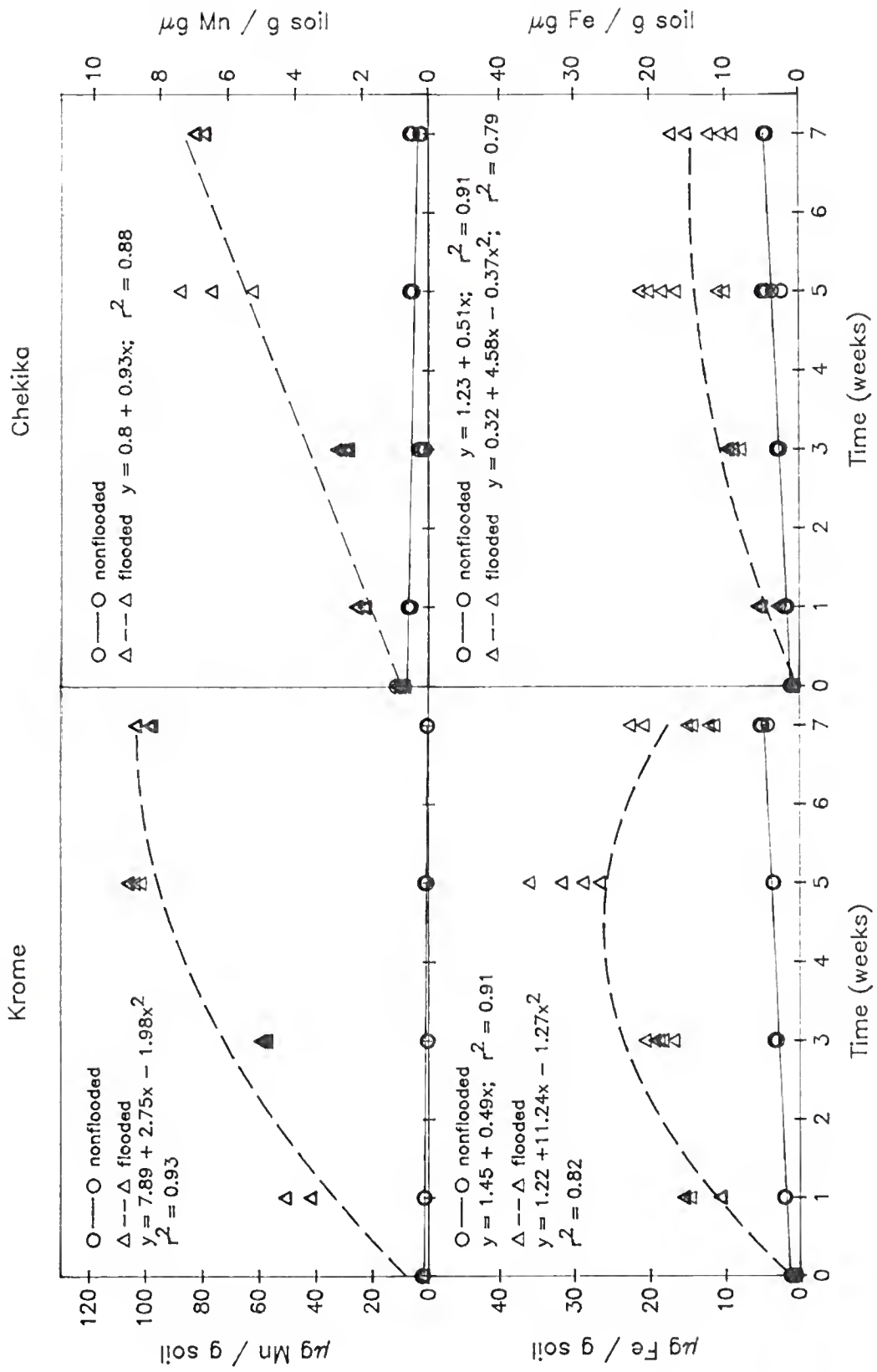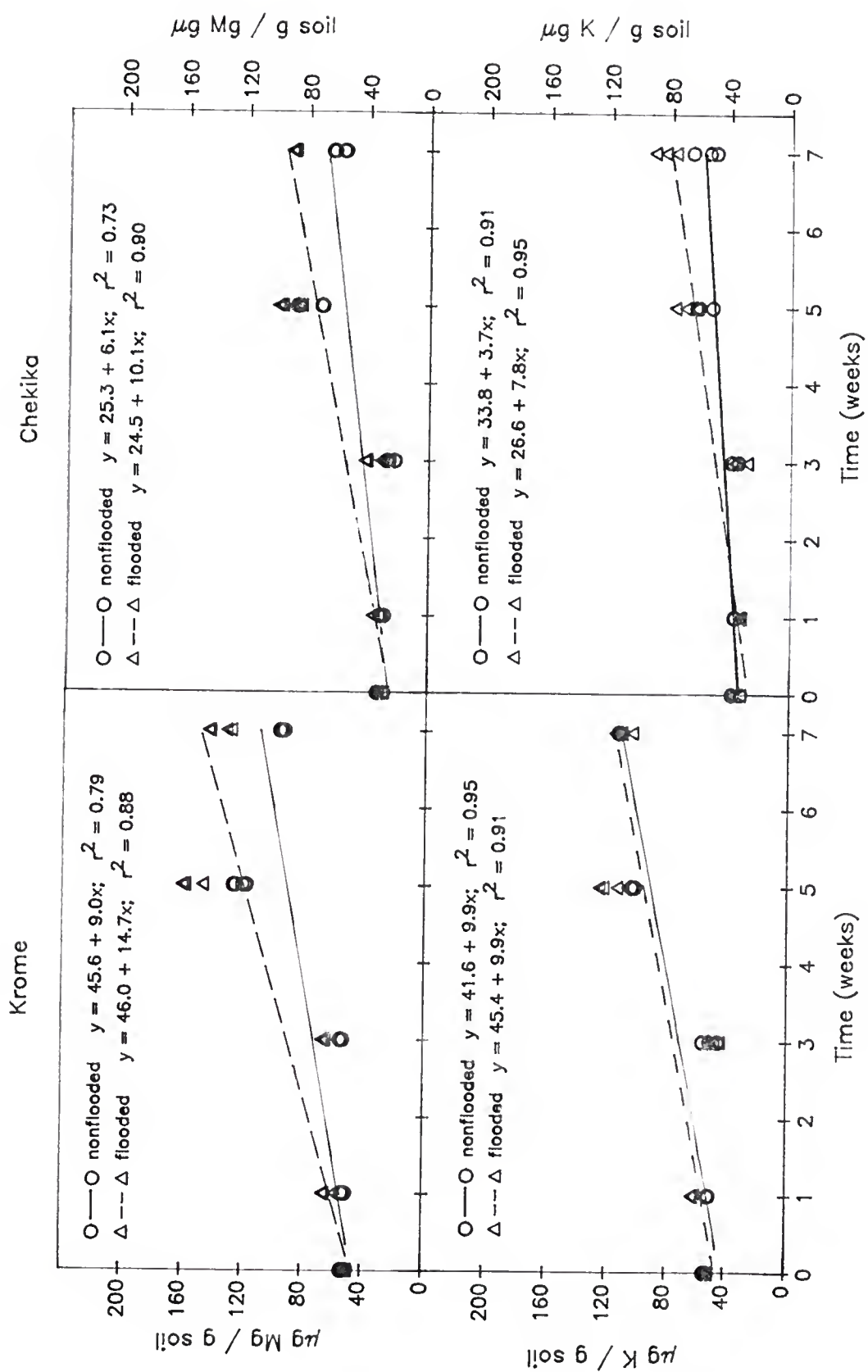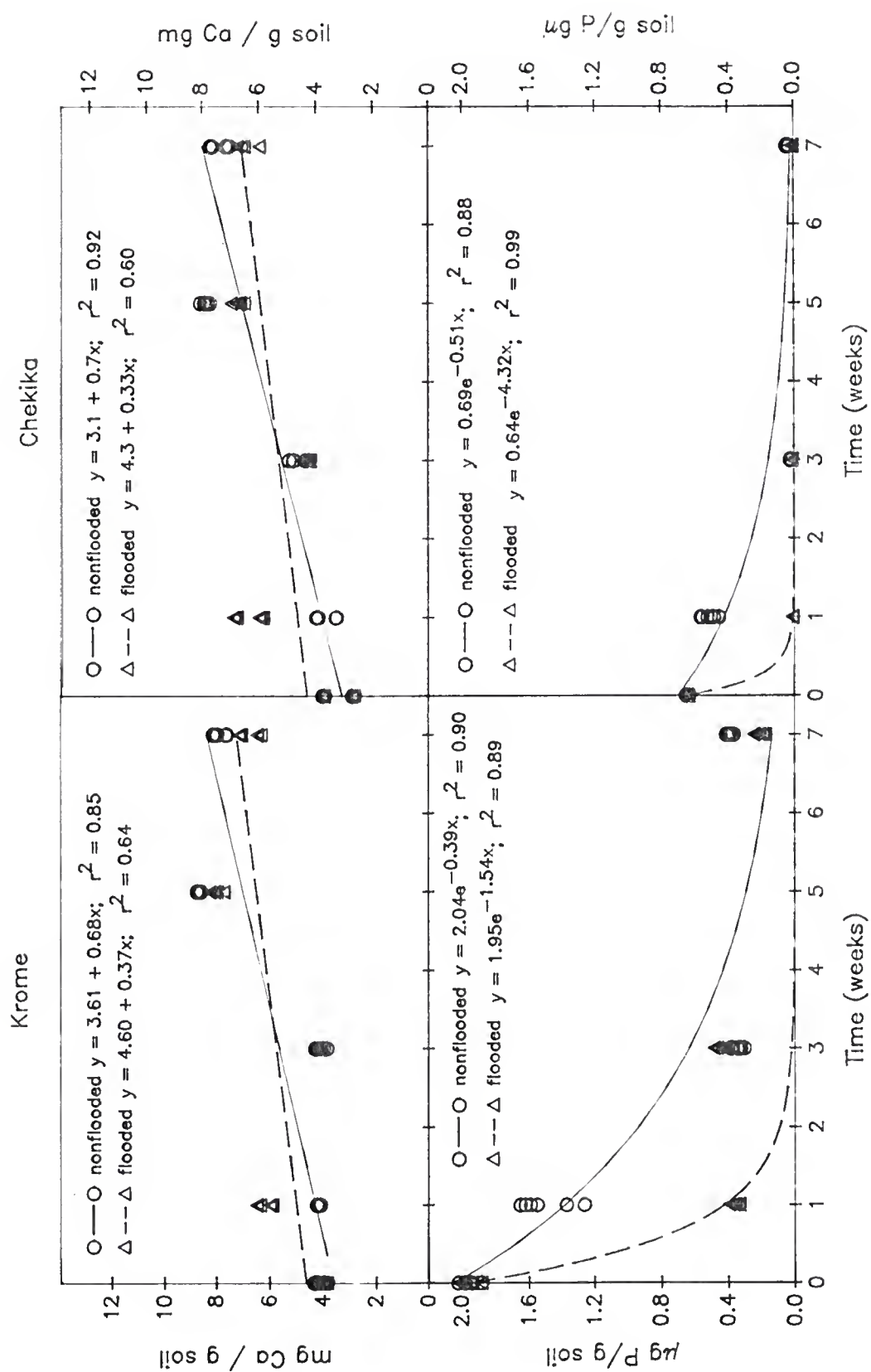## FLOODING, MINERAL NUTRITION AND NET GAS EXCHANGE OF MANGO TREES

Introduction

In many woody plants, waterlogging results in reduced nutrient

uptake and decreased leaf nutrient content due to increased root

mortality and reductions in root metabolism, transpiration and hydraulic

conductivity (Kozlowski and Pallardy, 1984; Labanauskas et al., 1971;

Schaffer et al., 1991). In some cases, however, flooding can increase

foliar nutrient concentrations (Hook, et al., 1983; Labanauskas et al.,

1968; Labanauskas et al., 1966 ; Olien, 1989; Slowik et al., 1979).

This may be due, in part, to flood-induced reduction and solubilization

of relatively insoluble soil compounds that are then more available to

plants (Kozlowski and Pallardy, 1984; Ponnamperuma, 1972).

Mango (Mangifera indica L.) production in the United States occurs

almost exclusively on calcareous flood-prone soils, and deficiencies of

minor elements, particularly Fe and Mn, are common in these soils

(Davenport, 1983; Malo, 1965; Schaffer et al., 1988). Although flooding

decreased leaf gas exchange and vegetative growth, I have observed

slight increases in net CO_2 assimilation of mango after short durations

of flooding (K.D. Larson, unpublished data). This may be due to

chemical changes that occur in flooded soil, since Fe and Mn are 10- to

50-fold more available when these calcareous soils are flooded. The

purpose of this study was to determine the effect of short-term flooding

on leaf nutrient concentration of mango trees grown in calcareous limestone soil, and to determine the relationship between leaf nutrition and gas exchange following short-term flooding.

Materials and Methods

Plant Material and Soil

'Peach' mango (Mangifera indica L.) trees were propagated from seed and transplanted into a sand media in 3.8-liter containers. Trees were trained to a single leader and fertilized monthly with 5 g of granular fertilizer, and 1.8 g of chelated Fe (6% Fe) (Sequestrene 138, Ciba Geigy Corp., Greensboro, NC 27419) applied as a soil drench. The granular fertilizer contained: 1.0% nitrate N; 4.6% ammoniacal N; 1.68% water-soluble organic N; 0.72% water-insoluble N; 1.32% available P; 7.47% water-soluble K; 3.0% Mg; 0.50% Fe; 0.07% Mn; 0.07% Zn; 0.03% B; and 0.03% Cu.

In June 1989, 60 uniform trees (mean height = 0.5 m) were transplanted into Krome very gravelly loam soil (loamy-skeletal, carbonatic, hyperthermic Lithic Rendoll) in 11.3-liter containers and grown outdoors. After transplanting, trees received 10 g of the granular fertilizer described above at monthly intervals. Trees were divided into 2 groups of 30 trees each immediately after transplanting. One group received chelated Fe (+Fe) applied as a soil drench at the rate of 5.0 g of chelate/tree/month for 7 months, while the other group was given no chelated Fe (-Fe). After 7 months, visual symptoms of Fe deficiency were observed in -Fe trees, but not in +Fe trees.

For all trees, stem diameter was determined 15 cm above the soil line prior to flooding and 91 and 182 days after the imposition of flooding treatments. Stem radial increase was calculated for each 3-month period.

Flooding Treatments

On 29 March, 1990 all trees in each fertilizer treatment were randomly exposed to one of three flooding treatments: 1) roots flooded for 10 days (F10); 2) roots flooded for 20 days (F20); and 3) nonflooded (NF = control) plants. The design was a 2 X 3 factorial (2 Fe fertilization rates X 3 flooding treatments) with 10 single-tree replicates per treatment in a split plot design. Iron treatment was the main plot and flooding treatment was the subplot. Flooding was accomplished by submerging trees in plastic tubs in tapwater and maintaining water levels ca. 10 cm above the soil surface. Nonflooded trees were irrigated 2-3 times each week to maintain soil moisture near container capacity. Ambient temperatures during the flooding period ranged from 12 to 30° C, and flooded soil temperatures averaged 23° C.

Soil redox potential (Eh) and pH were monitored periodically for six flooded trees from each Fe fertilization treatment, three trees from each of the F10 and F20 treatments. Soil redox potential was monitored at a soil depth of 15 cm using a $Ag^+/AgCl$ reference electrode (Model RC5, Jensen Instruments, Tacoma, Washington), an oxygen meter (Model P5E, Jensen Instruments), and four platinum-tipped microelectrodes, as described by Crane and Davies (1988). Soil pH was monitored with a pH meter (Model 5995-30, Cole Parmer Instruments, Inc., Chicago, IL).

Leaf Mineral Nutrition and Chlorophyll Content

Three days prior to flooding and 82 days after flooding treatments were imposed, total leaf chlorophyll content (Chl) was determined from eight 0.32-cm^2 leaf discs taken from 3 leaves at the mid-section of the most recently matured vegetative growth flush on all trees as described by Marini and Marini (1983). Two days after each chlorophyll determination, the same leaves were harvested and prepared for nutrient analysis as described by Schaffer et al. (1988). Foliar concentrations of K, Ca, Mg, Mn, Fe and Cu were determined by atomic absorption spectroscopy. Nitrogen was measured with a Kjeldahl apparatus, and N and P concentrations were determined colorimetrically with an autoanalyser (Technicon II, Tarrytown, NY).

For all trees, fertilizer applications were terminated for the duration of the experiment once flooding treatments were imposed. After flooding, all trees were watered as described for nonflooded trees.

Gas Exchange

Twelve days prior to flooding, one week after flooding was imposed, and at about monthly intervals for 6 months thereafter, net CO_2 assimilation (A) of single leaves was determined for all trees with a portable infrared gas analyzer (Analytical Development Co, Hoddeson, Herts., U.K.) as described by Schaffer and O'Hair (1987). All measurements were made between 1100 and 1400 hrs (EST) when photosynthetic photon flux (PPF) exceeded 500 μmol m^{-2} s^{-1}, which is above light saturation for net CO_2 assimilation of mango (Schaffer and Gaye, 1989). Air flow into the leaf chamber was 375 ml min^{-1}, CO_2 concentration in the chamber was 349 $\pm$ 7 μmol mol^{-1}, air temperature was

27.6 ± 5.3 C, and mean vapor pressure was 1.2 kPa (ranging from 0.9 to 2.1 kPa). Gas exchange calculations were based on those described by Jarvis (1971) and von Caemmerer and Farquhar (1981). Leaf gas exchange varied little among similar aged leaves of individual mango trees (data not shown). Therefore, one fully mature, sun-exposed leaf on the most recently matured growth flush of each tree was used for gas exchange determinations.

Data were analyzed by ANOVA and standard T-test.

Results

Soil Chemistry and Plant Growth

There was no effect of Fe fertilization on soil Eh or pH (P > 0.05). Therefore, Fe treatments were pooled for comparisons of Eh and pH among treatments. Anaerobic soil conditions (< 200 mv) (Ponnamperuma, 1972) developed one day after flooding (Fig. 4-1). Thereafter, Eh decreased little until day 10 and was about -100 mv by day 14. Prior to flooding, soil pH was about 7.4 (Fig. 4-1), and decreased to about 7.1 after 20 days of flooding.

There were no differences among treatments in stem radial growth over the course of the experiment (data not shown).

Leaf Chlorophyll Content and Mineral Nutrition

Total leaf chlorophyll content decreased over time for both Fe treatments, regardless of flooding treatments (Table 4-1). However, this decrease was not significant for flooded, -Fe plants. For both Fe

treatments, the decrease was greatest for the nonflooded plants, and least for plants that were flooded for 20 days.

Prior to flooding, mean Chl, and foliar Mn and Fe concentrations were about 1.3 - 1.5-fold greater for the +Fe trees than for the -Fe trees (Tables 4-1 and 4-2), whereas foliar K, Ca and Mg concentrations were 1.5 - 1.7-fold greater for -Fe trees than for +Fe trees (Tables 4-3 and 4-4). Prior to flooding, there were no differences in foliar N, P or Cu concentrations between -Fe and +Fe trees (Tables 4-3 and 4-4). There was no difference in foliar Zn concentration among Fe or flooding treatments at either sampling date (pooled mean for all treatments = 15.8 mg/kg; data not shown).

After imposition of flooding there were no significant interactions among Fe fertilization and flooding treatment (P > 0.05) with foliar concentrations of N, P, Mg, or Fe. Therefore, only main effects due to Fe fertilization and flooding are presented for these nutrients (Tables 4-2 and 4-3, respectively). Significant interactions among Fe fertilization and flooding treatment with regard to Chl and foliar Mn, K, Ca, and Cu concentrations (P < 0.05) are reported separately within each Fe fertilization treatment.

There was a significant decrease in foliar Mn concentration between sampling dates in the nonflooded, +Fe trees (Table 4-1). For +Fe trees, foliar Mn concentration was unaffected by flooding, although foliar Mn concentration tended to be higher with increase flooding duration. In contrast, in the -Fe trees, there were significant increases in foliar Mn concentration for the F10 and F20 treatments, but foliar Mn concentration was unaffected in the nonflooded treatment. The

greatest increase in foliar Mn concentration occurred with the longest flooding duration.

Foliar Fe concentration increased between sampling dates regardless of Fe treatment (Table 4-2) or flooding (Table 4-3). Due to the large variation in foliar Fe concentration of nonflooded plants at the second sampling date, the increase in Fe concentration was not significant for this treatment (Table 4-3). Almost three months after flooding treatments were imposed, there was no difference in foliar Fe concentration between +Fe and -Fe trees.

For both Fe treatments, flooding resulted in a significant increase in foliar Mg. Magnesium concentration increased for all flooding treatments, but the increase was greatest in trees exposed to 20 days of flooding (Table 4-2). Regardless of flooding treatment, foliar K and Ca concentrations increased over time in the +Fe trees, but were stable (nonflooded and F10 treatments) or decreased (F20 treatment) in the -Fe trees.

Although foliar N concentration decreased in the -Fe trees between sampling dates (Table 4-3), there was no significant effect of flooding on N (Table 4-2). For both Fe treatments there was a significant increase in foliar P over time (Table 4-2) regardless of flooding treatment (Table 4-3). For the +Fe trees, foliar Cu concentration increased irrespective of flooding treatment, but increases tended to be greater with increased flooding duration (Table 4-4).

Gas Exchange

Prior to flooding, mean net CO_2 assimilation of the +Fe trees was over 1.3 times greater than that of the -Fe trees (Figure 4-2).

Flooding resulted in rapid decreases in net CO_2 assimilation, regardless of Fe treatment, and recovery of net CO_2 assimilation after flooding was slow. Within each Fe treatment, there was no difference in net CO_2 assimilation between F10 and F20 treatments. For the -Fe trees, 184 days after flooding was imposed, F20 treatment net CO_2 assimilation was significantly greater than that of the control treatment. At the same time, for the -Fe trees, net CO_2 assimmilation of the F10 and F20 treatments were similar to that of the +Fe trees.

Discussion

The slow decrease in Eh of flooded soil may have been due to relatively cool ambient and soil temperatures, since at temperatures below 25° C Eh decreases at a slower rate than at higher temperatures (Ponnamperuma, 1972). The rate of decrease in flooded soil pH was slower than that observed in previous flooding studies with Krome very gravelly loam soil and may also have been affected by temperature (Ponnamperuma, 1972).

Mango tree stem radial growth has been correlated with canopy volume (unpublished data). Thus, the lack of difference among treatments in stem radial growth indicate no difference in canopy volume. Therefore, it is unlikely that differences in foliar nutrient concentrations among treatments were due to dilution effects resulting from vegetative growth differences.

To our knowledge, the critical foliar nutrient concentration ranges for optimal growth and productivity of mango trees have not been determined. However, Young and Koo (1971) working in Florida, and Gazit

(1969) working in Israel, reported foliar nutrient concentrations for healthy trees grown in calcareous soils. In our study, foliar N and P concentrations were similar to, but foliar Ca concentration was lower than those reported by Gazit (1969) and Young and Koo (1971). For the +Fe trees, foliar Fe concentration was similar to concentrations previously reported for healthy mango trees (Gazit, 1969; Young and Koo, 1971). As in our study, Gazit (1969) found much higher foliar K concentrations in iron deficient trees than in trees that were not Fe deficient. Foliar Zn concentration (pooled mean for all treatments = 15.8 mg/kg) was only about 10 - 20% of the mean foliar Zn concentration in healthy trees in Florida and Israel (Gazit, 1969; Young and Koo, 1971). In our study, although visual symptoms of Zn deficiency were not observed, the trees received minimal Zn fertilization and may have suffered from incipient Zn deficiency. Foliar Mg concentration of the -Fe trees was similar to that reported for healthy mango trees grown in limestone soil in Florida (Young and Koo, 1971).

Similar to our observations, seasonal variations in mango Chl have been reported previously (Schaffer and Gaye, 1989). Flooding stress often results in reduced Chl (Trought and Drew, 1980; Wallihan et al., 1961). Thus, the lack of a decrease in Chl between sampling dates for flooded, -Fe trees may be due to the flood-induced increases in foliar Mn and Fe concentrations observed for this treatment.

Increases in foliar Fe concentration have been observed for other woody plants exposed to flooded soil conditions (Hook, et al., 1983; Labanauskas et al., 1966, 1968; Olien, 1989; Slowik et al., 1979). This was presumably due to the flood-induced reduction of insoluble Fe compounds, making them more available to the plant (Ponnamperuma, 1972;

Kozlowski and Pallardy, 1984). Apparently, Fe deficiency resulted in a stronger Fe sink and greater Fe uptake in the Fe-deficient trees than in the nondeficient trees (Barber, 1979; Nye and Tinker, 1977; Pitman, 1965). The positive correlation between foliar concentrations of Fe and Mn and leaf chlorophyll content observed for mango has also been observed for many other species (Homann, 1967; Jacobsen and Oertli, 1956; Machold and Scholz, 1969; Spiller and Terry, 1980; Stocking, 1975; Terry, 1980).

Although Mg is an essential component of the chlorophyll molecule, Chl was not correlated with leaf Mg concentration (Tables 4-1, 4-2), perhaps due to the fact that only 15 to 20% of total plant Mg is associated with chlorophyll (Neales, 1956). Magnesium deficiencies are common in South Florida limestone soils due to the high pH and Ca saturation of the exchange complex. However, in flooded alkaline soils, dissolution of $MgCO_3$ and the increased concentration of reduced cations (Fe^{2+}, Mn^{2+}) in the soil solution can lead to displacement of Mg^{2+} from the exchange complex, thereby increasing its availabity (Reddy and Patrick, 1983).

The greater preflood foliar concentrations of K, Ca and Mg for the -Fe trees may have resulted from cation-anion balance effects (Kirkby, 1968). The -Fe trees had lower preflood foliar concentrations of Fe and Mn, and therefore may have required greater foliar concentrations of K, Ca and Mg to balance the negative charge of foliar anions. The significant decreases in foliar K and Ca concentrations for the -Fe trees exposed to 20 days of flooding may have also been due to ionic balance effects, since 20 days of flooding resulted in large increases in Fe, Mn and Mg for these trees.

Soil flooding frequently results in rapid decreases in NO_3^- concentration in the soil solution (Gambrell and Patrick, 1978; Ponnamperuma, 1984), due to leaching and denitrification. Decreases in soil NO_3^-, and the inhibition of ion uptake and transport by roots under anaerobic soil conditions (Trought and Drew, 1980) often result in flood-induced decreases in foliar N concentrations (Hook et al., 1983; Stolzy et al., 1975; Trought and Drew, 1980). With the flooded treatments, foliar N concentrations were stable, possibly due to the fact that only a small percentage of the N applied to the experimental trees was NO_3^--N, and flood-induced N losses from the soil were therefore minimized.

Foliar P concentration often decreases with soil flooding (Herath and Eaton, 1967; Hook et al., 1983; Kozlowski and Pallardy, 1984; Slowik et al., 1979; Stolzy et al., 1975). However, in alkaline soils where native P is not very soluble, flooding can increase P availability due to reduction of insoluble P compounds (Kozlowski and Pallardy, 1984). Thus, the lack of a decrease in foliar P for the flooded treatments may be related to increased P availability under flooded conditions. Additionally, to maintain an ionic balance, the observed increase in concentrations of foliar cations, particularly Mg and Fe, in all flooding treatments may have resulted in increased foliar concentration of anionic species such as PO_4^- (Kirkby, 1968).

With flooding, the decrease in soil pH, the reduction of Fe and Mn compounds in the soil and subsequent displacement of other cations from the exchange sites, and the production of organic complexing compounds can result in increased solubility of Cu in the soil solution (Kozlowski and Pallardy, 1984). For the +Fe, nonflooded trees, increased foliar Cu

concentration may be due to ionic balance effects (Kirkby, 1968), since the concentration of foliar Mn (another cationic species) decreased for this treatment. For the -Fe trees, the decrease, or lack of significant increases in foliar Cu may also be related to cationic-anionic balance effects, since -Fe trees tended to have large increases in concentration of certain foliar cations.

Prior to flooding, the greater net CO_2 assimilation for +Fe trees than for the -Fe trees was probably due to higher Chl and foliar Fe and Mn concentrations. Iron deficiency results in reductions in Chl, photosynthetic electron transport, chloroplast protein content, RuBP carboxylase/oxygenase activity, and reductions in the number of chloroplast grana and stromal lamallae (Shetty and Miller, 1966; Spiller and Terry, 1980; Stocking, 1975; Terry, 1980; Vesk et al., 1966). Manganese deficiency results in fewer chloroplasts per cell and chloroplasts with low chlorophyll contents (Homann, 1967). Prior to flooding, greater Chl and foliar Fe and Mn concentrations contibuted to greater net CO_2 assimilation in the +Fe trees. The increase in leaf gas exchange for iron-deficient trees exposed to 20 days of flooding may be related to the flood-induced increases in foliar micronutrient concentrations, particularly Mn, and lack of a decrease in Chl.

Conclusions

Although previous studies have shown that flooding results in transitory reductions in net gas exchange and vegetative growth of containerized mango trees (K.D. Larson, unpublished data), the data from this study indicate that short-term flooding of mango trees grown in

limestone soils results in significant increases in the concentration of some foliar nutrients and can also result in increased net CO_2 assimilation after floodwaters subside. Additional studies should be conducted to determine the potential of using short-term flooding as a management tool for reducing micronutrient deficiencies in mango trees grown in limestone soils.

Figure 4-1. Soil redox potential (Eh) and pH of Krome very gravelly loam soil as a function of flooding duration. Values represent mean Eh and mean pH ± S.E. of 12 flooded soils (6 from each Fe treatment) for the first 10 days of flooding, and 6 flooded trees (3 from each Fe treatment) for the final 10 days. Where not shown, S.E. bars are within the area of the symbol.
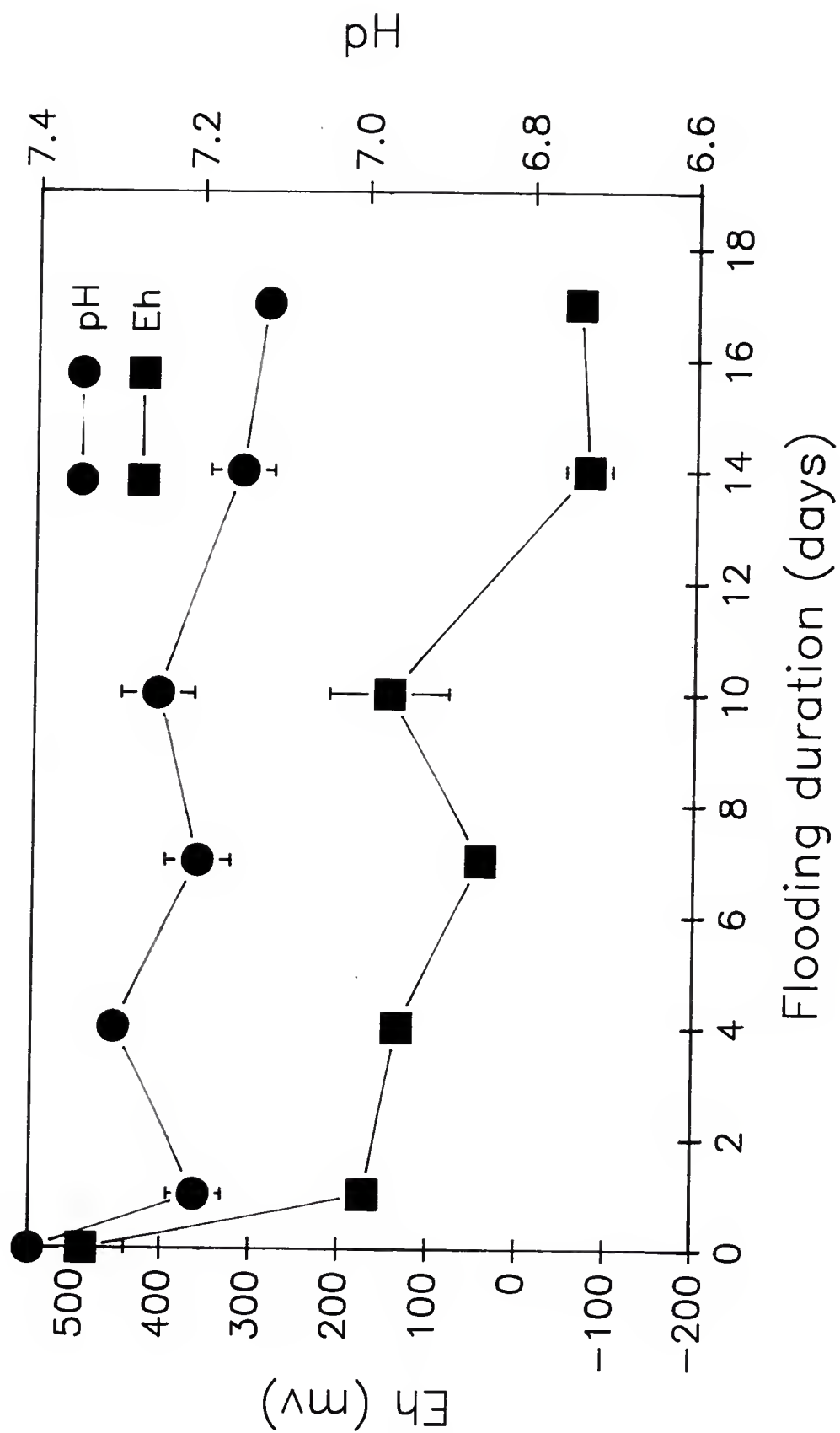
Figure 4-2. Mean net CO_2 assimilation of flooded and nonfloooded 'Peach' mango trees, grown with (+Fe) or without (-Fe) chelated iron fertilizer. Flooding treatments were imposed 28 March. Values represent means of 10 trees for each flooding treatment ± S.E. Where not shown, S.E. bars are within the area of the symbol.
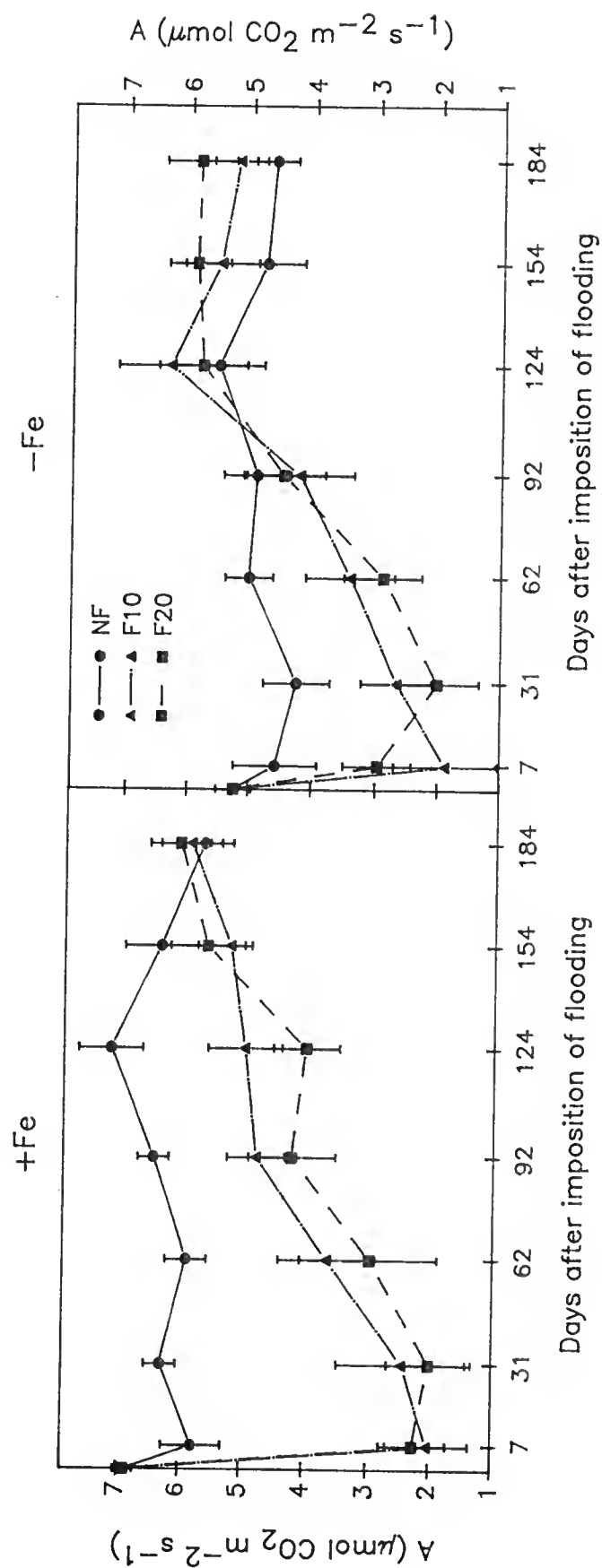
Table 4-1. Effect of flooding on total leaf chlorophyll content (Chl) and foliar Mn concentration of 'Peach' mango trees grown with (+Fe)or without (-Fe) chelated Fe.

Flood trt[z]	Chl (μg cm^{-2})			Mn (μg kg^{-1})		
	Pre trt[y]	Post trt[x]		Pre trt[w]	Post trt[v]	
		+Fe				
NF	20.43	14.73	**	65.10	15.20 c	**
F10	19.11	13.75	**	41.50	48.20 b	NS
F20	18.58	14.07	**	56.50	75.90 a	NS
		-Fe				
NF	12.37	8.77 b	**	39.80	32.70 b	NS
F10	12.13	10.22 ab	NS	41.10	82.10 a	*
F20	14.25	12.91 a	NS	45.96	114.30 a	**

Mean separation within rows by standard T-tests, n = 10 trees; *, ** indicate significant differences (P < 0.05 or 0.01, respectively) between pretreatment and posttreatment concentrations, NS indicates no significance.

Mean separation within columns for each Fe treatment by Duncan's Multiple Range Test (P < 0.05), n = 10 trees. Absence of letters indicates no significance.

[z] NF = nonflooded; F10 = flooded for 10 days; F20 = flooded for 20 days.

[y] Three days prior to imposition of flooding treatments.

[x] 82 days after imposition of flooding treatments.

[w] One day prior to flooding.

[v] 84 days after imposition of flooding.

Table 4-2. Effect of Fe fertilization on foliar concentrations of N, P, Mg and Fe of 'Peach' mango trees.

Fe trt[z]	Fe ($\mu g\ kg^{-1}$) Pre trt[y]	Fe ($\mu g\ kg^{-1}$) Post trt[x]	Mg (%) Pre trt	Mg (%) Post trt	N (%) Pre trt	N (%) Post trt	P (%) Pre trt	P (%) Post trt
+Fe	57.4	93.97 **	0.124	0.187 **	1.53	1.51 NS	0.104	0.134 **
-Fe	38.9	84.40 **	0.185	0.228 **	1.56	1.42 **	0.107	0.136 **
	**	NS	**	**	NS	*	NS	NS

Mean seperation within rows by standard T-tests, n = 10 trees; * and ** indicate significant differences (P < 0.05 or 0.01, respectively) between pretreatment and posttreatment concentrations within Fe treatments.

Mean seperation within columns by standard T-tests, n = 10 trees; * and ** indicate significant differences (P < 0.05 or 0.01, respectively) between Fe treatments, NS indicates nonsignificance.

z +Fe = fertilized with chelated Fe; -Fe = chelated Fe withheld.

y One day prior to flooding.

x 84 days after imposition of flooding treatments.

Table 4-3. Effect of flooding treatment on foliar concentrations of Fe, Mg, N and P of 'Peach' mango trees.

Fld trt[z]	Fe (µg kg^{-1}) pre trt[y]	post trt[x]		Mg (%) pre trt	post trt		N (%) pre trt	post trt		P (%) pre trt	post trt
NF	50.10	104.65	NS	0.152	0.194 b	*	1.57	1.47	NS	0.105	0.135 **
F10	48.35	74.70	**	0.158	0.200 b	**	1.54	1.44	NS	0.106	0.137 **
F20	46.05	88.20	**	0.154	0.230 a	**	1.53	1.48	NS	0.107	0.133 **

Mean seperation within rows by standard T-tests, n = 10 trees; * and ** indicate significant differences ($P < 0.05$ or 0.01, respectively) between pretreatment and posttreatment concentrations, NS indicates nonsignificance.

Mean seperation within columns by Duncan's Multiple Range Test ($P < 0.05$), n = 10 trees; absence of letters indicates no significant differences.

[z] NF = nonflooded; F10 = flooded 10 days; F20 = flooded 20 days.

[y] One day prior to flooding.

[x] 84 days after imposition of flooding treatments.

Table 4-4. Effect of flooding on foliar K, Ca and Cu concentrations of 2-year-old 'Peach' mango trees grown with (+Fe) or without (-Fe) chelated Fe.

Flood trt[z]	K (%) Pre trt[y]	Post trt[x]		Ca (%) Pre trt	Post trt		Cu (μg kg^{-1}) Pre trt	Post trt	
				+Fe					
NF	0.89	1.11	**	0.738	1.135 a	**	4.20	12.30	*
F10	0.91	1.11	**	0.764	0.985 b	**	3.70	17.90	*
F20	0.91	1.08	**	0.643	0.992 b	**	3.90	19.10	**
				-Fe					
NF	1.60	1.45 a NS		1.164	1.072 a NS		4.00	7.10 b NS	
F10	1.36	1.25 b NS		1.122	0.793 b NS		4.30	2.40 a **	
F20	1.58	1.24 b *		1.281	0.807 b **		4.50	6.80 a NS	

Mean seperation within rows by standard T-tests, n = 10 trees; * and ** indicate significant differences (P < 0.05 or 0.01, respectively) between pretreatment and posttreatment concentrations within Fe treatments, NS indicates nonsignificance.

Mean seperation within columns within Fe treatments by Duncan's Multiple Range Test (P < 0.05), n = 10 trees. Absence of letters indicates no significance difference.

[y] NF = nonflooded; F10 = flooded for 10 days; F20 = flooded for 20 days.

[x] One day prior to flooding.

[w] 84 days after imposition of flooding treatments.

CHAPTER 5
FLOODING, LEAF GAS EXCHANGE AND GROWTH OF MANGO TREES IN CONTAINERS

Introduction

Among the most rapid physiological responses of fruit trees to flooding are a reduction in stomatal conductance (g_s) and net CO_2 assimilation (A), (Andersen et al., 1984a, 1984b; Crane and Davies, 1989; Davies and Flore, 1986c; Schaffer and Ploetz, 1989; Smith and Ager, 1988; Syvertsen et al., 1983). Woody plants often exhibit a decrease in A and g_s within 1 to 3 days after flooding, although longer flooding durations are required for reductions in growth (Andersen et al., 1984a; Crane and Davies, 1989).

Tolerance of mango trees to flooding is not well known. Some reports indicate that mangos require good soil drainage for adequate growth and yield (Alfonsi, 1980; Samson, 1986), whereas other reports indicate that they are flood tolerant (Chandler, 1958; Jawanda, 1961; Young and Sauls, 1981). Therefore, experiments were initiated to determine the physiological and growth responses of mango trees to flooding using leaf gas exchange, leaf water potential, vegetative growth and tree survival as stress indicators.

Materials and Methods

Flooding, Net Gas Exchange and Vegetative Growth (Experiment I)

Thirty, 4-year-old 'Tommy Atkins' mango trees, about 2.25 m in height (15 on 'Turpentine' rootstock and 15 on an unknown seedling rootstock) were grown outdoors in 57-liter containers with Krome very gravelly loam soil (loamy-skeletal, carbonatic, hyperthermic Lithic Rendoll). Trees were exposed to three treatments in October, 1989; 1) nonflooded (control), 2) flooded for 14 days (14DF), or 3) flooded for 28 days (28DF). Five single tree replicates of each rootstock were used for each experimental treatment. Thus, there was a 2 x 3 factorial arrangement of treatments (2 rootstocks, 3 flooding treatments) that was replicated five times in a split plot design, with rootstock as the main-plot and flooding treatment as the subplot. Plants were flooded by submerging the containers in plastic-lined metal tubs filled with tap water. Water levels in the tubs were maintained about 10 cm above the soil surface. Control trees were watered about twice a week to maintain soil moisture near container capacity.

Diurnal air temperatures fluctuated between 22 and 34 C during the experiment. Initially, soil temperatures were higher for the nonflooded than the flooded treatments, but after 3 days mean soil temperatures at 5 cm depth were about 34 C for all treatments.

For flooded trees, soil redox potential (Eh) was monitored periodically at a soil depth of 15 cm using a silver/silver chloride reference electrode (Model RC5, Jensen Instruments, Tacoma, Washington), an oxygen meter (Model P5E, Jensen Instruments) and four platinum-tipped microelectrodes, as described by Crane and Davies (1988). The platinum

tips of the microelectrodes were fused to a 3 mm brass alloy rod and the junction sealed in epoxy resin (Bohn, 1971; Mann and Stolzy, 1971). Prior to use, accuracy of each microelectrode was checked by measuring the electrical potential of pH-buffered quinhydrone solutions (Bohn, 1971).

For all trees, A, g_s, transpiration (E), internal CO_2 concentration (C_i) and leaf temperatures were determined with a portable infrared gas analyzer (Analytical Development Co, Hoddeson, Herts., U.K.), as previously described (Schaffer and O'Hair, 1987). All gas exchange determinations were made at photosynthetic photon flux > 500 μmol m^{-2} s^{-1}, which is above light saturation for mango (Schaffer and Gaye, 1989). Air flow into the leaf chamber was 375 ml min^{-1}, CO_2 concentration was 346 $\pm$ 9 μmol mol^{-1}; air temperature was 29.8 $\pm$ 5.5 C; and mean vapor pressure was 1.1 kPa (ranging from 0.9 to 2.1 kPa). Gas exchange calculations were based on those described by Jarvis (1971) and von Caemmerer and Farquhar (1981). Repeated measurements showed little difference in net gas exchange among leaves of similar age in individual mango trees (data not shown). Therefore, one fully mature, sun-exposed leaf on the most recent, mature growth flush of each tree was used for gas exchange determinations. Measurements were made between 1000 and 1300 hr (EST) prior to flooding, at 2 and 5 days of flooding, and at about weekly intervals for 65 days thereafter.

Stem radial growth was determined by measuring stem circumferences 10 cm above the graft union prior to flooding and 28, 56 and 84 days after flooding was imposed. Shoot extension growth was determined on two actively-growing, sun-exposed shoots per tree. Shoots were measured

prior to flooding and extension growth determined 84 days after flooding was imposed.

Gas exchange and growth data were analyzed by ANOVA ($P \leq 0.05$).

Flooding and Leaf Water Potential (Experiment II)

Twelve 4-year-old 'Tommy Atkins' mango trees, six on 'Turpentine' rootstock and six on a seedling rootstock, about 2.25 m in height, were grown in 57-liter containers in Krome very gravelly loam soil. On 7 Dec., 1989, trees were subjected to two flooding treatments as described in Expt. I: 1) nonflooded (control), and 2) continuously flooded for 14 days. Three single tree replicates of each rootstock were used for each treatment. Thus, there was a 2 x 2 factorial arrangement of treatments, replicated 3 times in a split plot design with rootstock as the main-plot and flooding treatment as the subplot. Diurnal air temperatures fluctuated between 10 and 24 C during the experiment, and flooded soil temperatures averaged 16 C.

Prior to flooding and at biweekly intervals for 2 weeks thereafter, A, g_s, E and C_i were determined at 1000-1300 hr for each tree. Gas exchange determinations were made as described in Expt I., except that temperature was 24.5 $\pm$ 4.4 C, CO_2 concentration was 345 $\pm$ 6 μmol mol^{-1}, and mean vapor pressure was 0.90 kPa (ranging from 0.42 to 1.40 kPa) in the leaf chamber. Immediately following gas exchange determinations, mid-day (1200-1400 hr) leaf water potentials were determined on three sun-exposed leaves of each tree with a pressure chamber (Model 3000, Soil Moisture Equipment Corp., Sta. Barbara, CA) as described by Scholander et al. (1965). Data were analyzed by a standard t-test ($P \leq 0.05$).

Net Gas Exchange During the Early Stages of Flooding (Experiment III)

To examine the effects of flooding on gas exchange during the early stages of flooding, ten, 1-year-old 'Peach' seedling mango trees, about 60 cm in height, were grown in 7.5-liter containers in peat:perlite (1:1 v/v). Five replicate plants were flooded on 6 Sept., 1989 by submerging the containers in tap water in plastic tubs, and five replicate plants were maintained nonflooded. Nonflooded plants were maintained as described previously, but water levels were maintained about 5 cm above the soil surface for flooded plants. The experimental design was a randomized complete block, with one tree from each treatment in each of five blocks. Determinations of A, g_s, E and C_i were made on two fully expanded, sun-exposed leaves of the most recent, mature growth flush of each tree at 1300 hr, immediately before plants were flooded. Thereafter, determinations were made at 1300 hr on day 1 of flooding, at 1000, 1300 and 1600 hr on days 2 and 3, and at 1000 hr on day 4 of flooding. For all trees, gas exchange was monitored as described in Expt. I, except for the following leaf chamber conditions: CO_2 concentration was 340 ± 9 μmol mol^{-1}, temperature was 31.4 ± 5 C, and mean vapor pressure was 0.94 kPa (ranging from 0.53 to 1.47 kPa). Data were analyzed by a standard t-test ($P \leq 0.05$).

Flooding and Growth (Experiment IV)

One-year-old 'Peach' seedling mango trees about 70 cm in height were grown in 11.5-liter containers in Krome very gravelly loam soil. Fifty trees were divided into four categories on the basis of height and basal stem diameters. Equal numbers of plants were randomly selected

from each size category and placed into five groups of 10 plants each, so that there was no difference among the groups in mean height or stem diameter. One randomly selected group was immediately harvested for determination of leaf area, total shoot length, length of new shoot growth flushes, and fresh and dry weights of leaves, new growth flushes, total shoot and roots, and for calculation of shoot:root ratios. The remaining groups were randomly assigned two treatments 1) flooded by submerging the containers in plastic tubs; or 2) nonflooded (control), both as described in Expt. III. Thus, two replicates of 10 sample trees were assigned to each treatment in a randomized complete block design. After 2 and 4 weeks of flooding, one group of plants in each treatment (flooded and nonflooded) was harvested. Mean leaf area (portable leaf area meter, Model LI-3000, LI-COR, Inc., Lincoln, NE 68504), total shoot length and length of new shoot growth flushes were determined for trees in all groups upon harvest. Plants were oven-dried at 60 C for 4 days and mean leaf dry weight, total shoot dry weight, dry weight of new shoot growth flushes, root dry weight, and root:shoot ratio were determined. Data were analyzed by a standard t-test ($P \leq 0.05$).

Results

Experiment I

Within 3 days of flooding, mean Eh of the flooded soil was +26 mv, indicative of anaerobic soil conditions (Gambrell and Patrick, 1978), and soil pH was 7.4. After 21 days of flooding, Eh and pH had stabilized at -150 mv and 7.0, respectively.

There was no interaction between rootstock and treatment for any of the variables measured ($P \leq 0.05$). Therefore, all 10 trees in a given treatment were pooled for statistical analyses. Leaf wilting and desiccation were observed for nine flooded trees within 3-4 days. With the exception of these nine trees (five from the 14DF treatment, four from the 28DF treatment), lenticel hypertrophy was observed on submerged stems of all flooded trees within 5-7 days. The nine trees exhibiting leaf dessication and shoot die-back were eliminated from the experiment by day 14.

Within 2 days of flooding, A of flooded trees became negative, and C_i, g_s and E and were 109%, 62% and 75% that of the nonflooded trees, respectively (Fig. 5-1). By day 58 (44 days after removal of plants from flooding), A, g_s and E of trees of the 14DF treatment were similar to those of the controls, decreased on day 64 and recovered again by day 70 (Fig. 5-1). By day 70, A, g_s and E of trees in the 28DF treatment were lower, and C_i was higher, than that of either the controls or the trees in the 14DF treatment (Fig. 5-1). Leaf temperatures of flooded plants were 1-2 C higher than leaf temperatures of nonflooded plants (data not shown).

Twenty-eight days after submergence, stem radial growth of trees in the 14DF and 28DF treatments was similar, but was 40% and 59%, respectively, of that of the nonflooded trees (Fig. 5-2). Fifty-six days after submergence, stem radial growth of trees in the 14DF and 28DF treatments was 31% and 46%, and by day 84 was 37% and 45%, respectively, of that of the nonflooded trees. There was no difference among treatments in shoot extension growth (data not shown).

After several weeks, infestations of bark-boring ambrosia beetles (<u>Xyloborus</u> spp., Coleoptera:Scolytidae) were noted in all flooded trees. This is often indicative of elevated ethanol concentrations in the xylem sap (Cade et al., 1970). No infestations occurred on nonflooded trees.

Experiment II

Rootstock did not effect water potential or net gas exchange of flooded and nonflooded trees ($P < 0.05$). Therefore, the six trees in each treatment were pooled for statistical analyses. For flooded trees, A decreased within 7 days of flooding (data not shown) and remained lower than that of the nonflooded trees for the remainder of the experiment. Flooding had no influence on leaf water potential, which averaged - 0.2 MPa, over the course of the experiment (data not shown). There were no visual symptoms of plant stress, such as leaf dessication or wilting, over the course of the experiment. Lenticel hypertrophy was noted on the submerged stems of 5 of the 7 flooded trees after about 10 days of flooding.

Experiment III

Flooded trees had simultaneous decreases in A, E and g_s, and an increase in C_i, by the morning of the third day of flooding (Fig. 5-3). In general, the difference in A between flooded and nonflooded plants decreased over the course of day 3 before increasing by day 4. Hypertrophied lenticels were observed at the floodline of stems of all flooded trees after 4-5 days of flooding.

Experiment IV

Leaf area, leaf dry weight, total shoot length, length of new growth flushes, dry weight of new growth flushes (data not shown) and total shoot dry weight (Fig. 5-4) were similar for flooded and nonflooded trees on any harvest date. Two and four weeks after submergence, root dry weights of flooded trees were significantly reduced, and were 76% (week two) and 66% (week four), respectively, of the nonflooded trees (Fig. 5-4). The initial shoot:root ratio was 2.38. After 2 weeks, shoot:root ratios of nonflooded and flooded trees were 2.72 and 3.80, respectively. By week 4, shoot:root ratios were 2.79 and 4.18 for nonflooded and flooded trees, respectively. There was no tree mortality in any treatment, and hypertrophied lenticels were observed in all flooded trees after 3-4 days of flooding.

Discussion

Greater tree mortality and a more rapid decrease in A were observed in Expt. I than in a previous study of mango flooding (unpublished data), or than in Expt. II. Although Expt. I and the previous study were conducted under similar environmental conditions, trees in the previous study had been recently transplanted into 57-liter containers, whereas trees in Expt. I were maintained in the same containers for 1.5 years, and were more root-restricted.

In Expt. II, A was not reduced until 7 days after submergence (data not shown), and visible symptoms of flooding stress (i.e., leaf desiccation, wilting) were not observed in any of the flooded trees. The cooler temperatures and shorter days during this experiment may have

moderated the flooding response. Slower growth rates than in previous experiments (data not shown) and reduced shoot and root respiration rates (not measured) due to cooler temperatures may have also affected the flooding response.

The stomatal response of flooded mangos in the present study (Fig. 5-1) differs from that of flood-tolerant species in which stomata reopen after 1-2 weeks of flooding (Kozlowski and Pallardy, 1984). Flood-induced stomatal closure has been attributed to decreases in leaf water potential resulting from decreased water uptake by the roots (Heinicke, 1932; Kozlowski and Pallardy, 1984), possibly as a result of decreased cell membrane permeability under anaerobiosis (Bradford and Hsiao, 1982). However, as in Expt. II, stomatal closure of flooded plants occurred without reductions in leaf water potential (Andersen et al., 1984b; Bradford and Hsiao, 1982; Kozlowski and Pallardy, 1984; Smith and Ager, 1988).

In some flooding studies, decreases in A have been attributed primarily to stomatal closure (Kozlowski and Pallardy, 1984). In the present study, the increase in C_i, concommitant with decreased A and g_s suggested that non-stomatal factors may have been influencing carbon assimilation (Farquhar and Sharkey, 1982).

Although a previous study showed a reduction of mango shoot extension growth with long-term (110 days) flooding (K.D. Larson, unpublished data), the shorter durations of flooding in Expt. I were apparently insufficient to reduce shoot extension growth. However, similar to previous observations (K.D. Larson, unpublished data) stem radial growth was affected by flooding in the present study. Since mango growth flushes are often restricted to certain shoots in one part

of the tree (Young and Sauls, 1981), stem radial growth measurements are a more sensitive indicator of tree growth than are measurements of shoot extension growth. An increased shoot:root ratio has often been observed in flooded woody plants, reflecting a greater sensitivity of root than shoot growth to flooding stress (Kozlowski, 1984). Inhibition of root growth with flooding is characteristic of flood-intolerant species (Kozlowski, 1984).

Lenticel hypertrophy occurs in several woody plant species subjected to flooding (Andersen et al., 1984a; Kawase, 1981; Kozlowski, 1984) and is thought to enhance O_2 diffusion to roots (Kozlowski, 1984), or eliminate potentially toxic metabolites such as ethanol, acetaldehyde or ethylene (Chirkova and Gutman, 1972). Development of hypertrophied lenticels, however, does not necessarily confer flood-tolerance. Andersen et al. (1984a) observed lenticel hypertrophy on submerged stems of flood-intolerant Prunus persica. Profuse lenticel hypertrophy occurred on stems of mango trees that survived flooding, but there was little or no stem hypertrophy with mango trees that died. Furthermore, when hypertrophied lenticels of flooded mango trees were covered, the trees died within three days (K.D. Larson, unpublished data). Thus, hypertrophied lenticels appear necessary for mango tree survival under prolonged flooding, but their exact role in gas exchange or in the elimination of metabolic end-products is not clear.

Conclusions

The ability of mango trees to survive prolonged flooding is variable and may be related to environmental conditions and the

development of hypertrophied lenticels in individual trees. In previous studies, mango trees survived flooding for 110 days or more. For trees that survive flooding, the reductions in gas exchange and stem radial growth, and the slow post-flood recovery with respect to gas exchange and growth, indicate that this species is able to adapt to flooded soil conditions, but is not highly flood-tolerant.

Fig. 5-1. Mean net CO_2 assimilation (A), stomatal conductance for CO_2 (gs), internal CO_2 concentration (Ci), and transpiration (E) of 'Tommy Atkins' mango trees flooded for 14 and 28 days, or nonflooded. Vertical lines represent pooled MSD according to Waller-Duncan K-ratio T-test (P < 0.05).
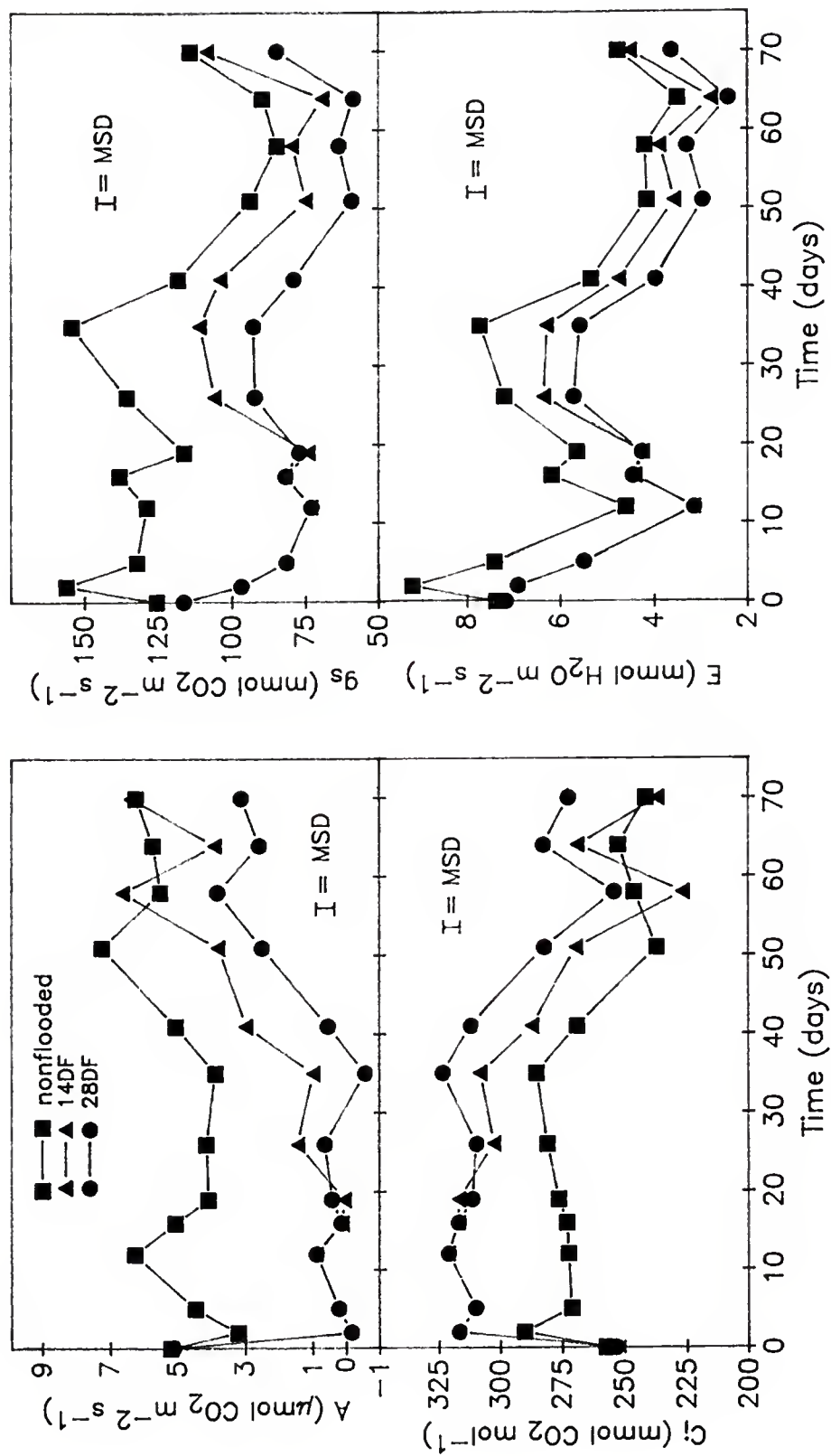
Fig. 5-2. Mean radial stem growth of 'Tommy Atkins' mango trees flooded for 14 and 28 days, or nonflooded. Different letters denote significant difference between treatments (P < 0.05).
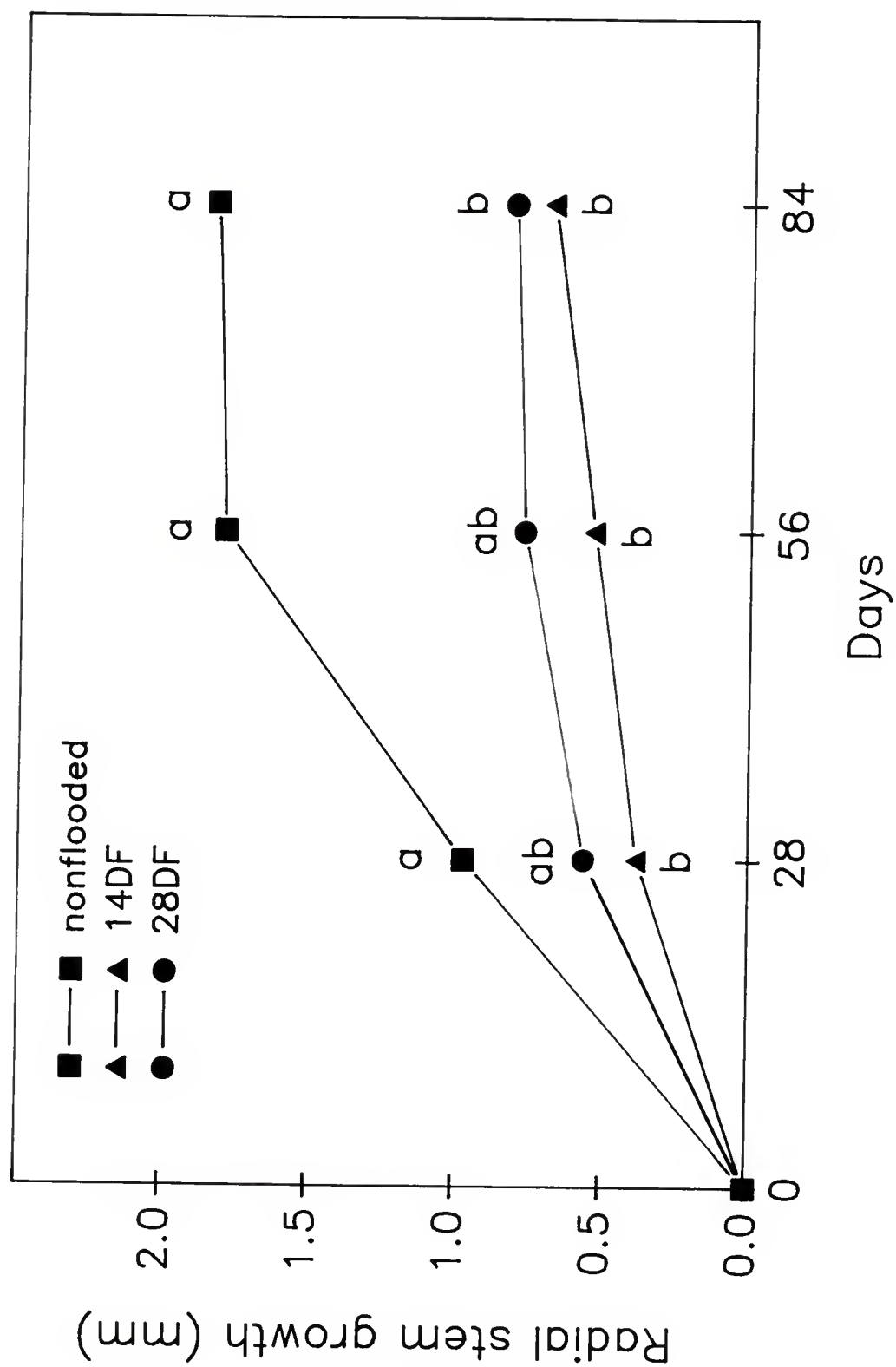
Fig. 5-3. Mean net CO_2 assimilation (A), stomatal conductance for CO_2 (gs), internal CO_2 concentration (Ci), and transpiration (E) of flooded and nonflooded 'Peach' mango trees. Asterisks denote significant difference between treatments ($P < 0.05$).
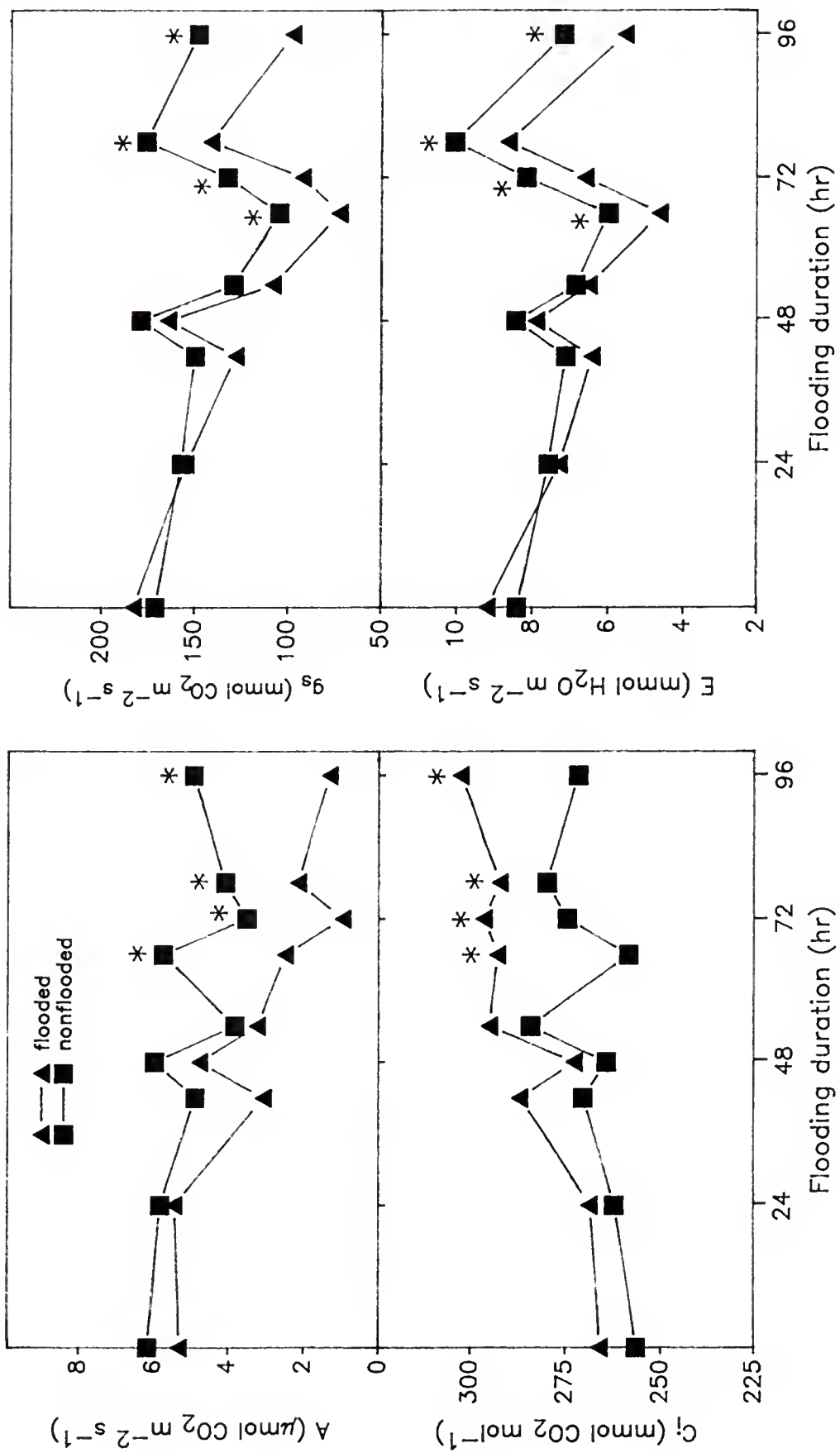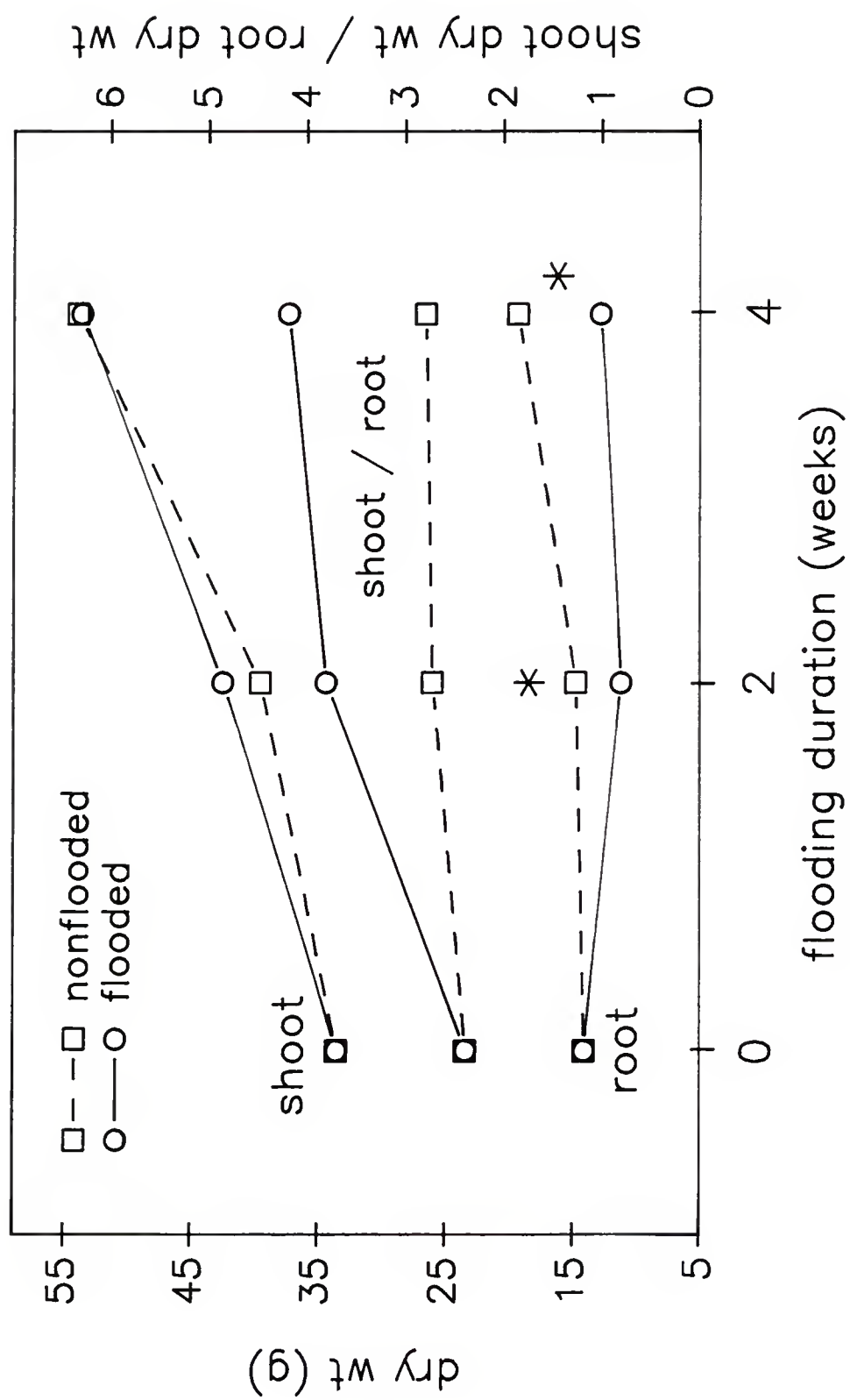
Fig. 5-4. Mean shoot and root dry weights, and shoot dry wt/root dry wt ratios of flooded and nonflooded 'Peach' mango trees. Asterisks denote significant difference between treatments ($P < 0.05$).

CHAPTER 6
FLOODWATER TEMPERATURE AND STEM LENTICEL
HYPERTROPHY IN MANGO TREES

Introduction

Lenticel hypertrophy (intumescence) has been observed on stems of several woody plant species under flooded conditions (Andersen et al., 1984; Angeles, 1990; Angeles, et al., 1986; Hook et al., 1970; Hook and Scholtens, 1978; Kawase, 1981; Kozlowski, 1984; Sena Gomes and Kozlowski, 1988; Tang and Kozlowski, 1984). Hypertrophic stem lenticels may allow internal oxygen diffusion to flooded roots (Kozlowski, 1984), or function as excretory sites for potentially toxic metabolites such as ethanol and acetaldehyde formed in the roots during anaerobic respiration (Chirkova and Gutman, 1972).

With mango, hypertrophic lenticels have been observed on stems of trees that survived soil flooding, but not on trees that died as a result of flooding stress (see Chapter Five, page 67). When hypertrophic lenticels of flooded mango trees were sealed, trees died within three days (K.D. Larson, unpublished data). Thus, it appears that hypertrophic lenticels of mango are necessary for tree survival under flooded soil conditions, although their specific role has not been elucidated.

Lenticel hypertrophy results from increased phellogen activity, cell enlargement, and cell elongation (Angeles, 1990; Kawase, 1981).

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These growth processes are temperature dependent. For example, phellogen activity of _Ailanthus altissima_, _Fraxinus pennsylvanica_, and _Robinia psuedacacia_ increased with increasing temperature (Borger and Kozlowski, 1972), since cell growth involves temperature-dependent enzymatic reactions. However, high soil and air temperatures also typically increase flooding stress and reduce plant survival (Abbott and Gough, 1985; Catlin et al., 1977; Childers and White, 1950; Crane and Davies, 1989; Davies and Flore, 1986a; Davies and Wilcox, 1984; Heinicke, 1932; Olien, 1987).

Anatomical and morphological development of hypertrophic stem lenticels have been characterized for many flooded woody plant species, including angiosperms (e.g. _Salix nigra_, _Populus deltoides_, _Fraxinus pennsylvanica_, _Quercus macrocarpa_, and _Platanus occidentalis_), and gymnosperms (e.g. _Pinus ponderosa_, _Pinus resinosa_, and _Larix laricina_ (Angeles, 1990; Angeles et al., 1986; Hook, et al., 1971; Hook and Scholtens, 1978; Kozlowski et al., 1991). However, to our knowledge, the influence of floodwater temperature on lenticel hypertrophy of trees has not been reported. The objective of this study was to characterize the changes in anatomy and morphology of stem lenticels of mango as affected by floodwater temperature.

Materials and Methods

Eighteen, one-year-old 'Peach' seedling mango trees were grown in a peat:sawdust:pine bark (1:1:1 v/v/v) media (pH 6.0) in 3.75-liter plastic pots in a glasshouse. The trees were randomly divided into three temperature treatments in March 1989, at which time average tree

height was 1.0 m. Pots were submerged in tap water in plastic containers enclosed in temperature-controlled flooding chambers in a laboratory (Gilreath et al., 1982). Soil, floodwater, and air temperatures within the flooding chambers were maintained at either 15, 22.5, or 30 $\pm 2^\circ$ C. Tap water adjusted to the specified temperature was added daily to each container to maintain floodwater at a level 10 cm above the soil surface. The foliated portion of the stems (upper 0.5 m of the trees) protruded through the lids of the chambers. A 400-watt mercury vapor lamp and four 100-watt incandescent light bulbs were positioned above each chamber to expose the foliage to a 10-hour photoperiod. Photosynthetic photon flux (PPF) in the upper part of the tree canopy was approximately 750 μmol m^{-2} s^{-1}, as determined with a selenium photo cell attached to a Parkinson leaf chamber (Analytical Development Co., Hoddeson Hertz., England). This PPF is above the light saturation point for photosynthesis of individual mango leaves (Schaffer and Gaye, 1989). Air temperature and relative humidity in the laboratory ranged from 22 to 34° C, and 28 to 45%, respectively.

Soil redox potential (Eh), pH, and dissolved oxygen content of the floodwater were monitored for each plant prior to flooding, at daily intervals during the first 4 days of flooding, and at 3-day intervals thereafter. Redox potential was determined at a depth of 10 cm using an oxygen diffusion meter (Model P5E, Jensen Instruments, Tacoma, Washington), with a Ag$^+$/AgCl reference electrode, and 4 platinum-tipped microelectrodes (Crane and Davies, 1988). Soil pH was monitored with a pH meter (Model 5995-30, Cole-Parmer Instruments, Chicago, IL), and floodwater O_2 content was monitored with an oxygen probe and meter (Model 5946-10, Cole-Parmer Instruments, Chicago, IL).

Prior to flooding, and at 24-hour intervals for 13 days thereafter, the development of lenticel hypertrophy was visually determined for all trees. Hypertrophic lenticels were readily distinguishable by a widening of the lenticel pore, and exposure of the white parenchymatous filling tissue. Based on detection of this filling tissue, hypertrophic lenticel density was determined daily in randomly selected 1-cm^2 stem sections within 1.5 cm of the floodline of each tree. Data pertaining to the number of hypertrophic lenticels per unit area were analyzed by non-linear regression using the Gompertz Logistical Growth Model (Clow and Urquhart, 1974).

In conjunction with daily visual observations of hypertrophy, a 0.5 cm^2 piece of bark, consisting of phloem, cortex, and periderm tissues, was excised with a razor blade from an area of the stem within 1.5 cm of the floodline of five trees in each treatment. A sixth tree in each treatment remained intact to determine whether wounding had an effect on lenticel hypertrophy or tree survival. Excised tissues were fixed in formalin acetic acid, dehydrated in alcohol, and embedded in paraffin. Tissues were sectioned with a rotary microtome at a thickness of 10 μm, stained with safranin and fast green, and mounted on microscope slides with Permount (Johansen, 1940). Photomicrographs of representative tissue sections were taken with a Nikon Optiphot Microscope with a Nikon AFX camera attachment.

Plants were removed from the flooding chambers after 13 days, and the experiment was repeated. Two plants from the original 15° C treatment were maintained submerged at 15° C for a total of 28 days, and then were transferred to 30° C floodwater. For a given floodwater temperature treatment, there were no differences between experiments in

regard to hypertrophic lenticel density or mean number of days required

for the development of lenticel hypertrophy (P > 0.05). Therefore, data

regarding hypertrophic lenticel density and mean number of days for

required for the development of hypertrophy were pooled for the two

experiments.

Results

Floodwater Oxygen Content and Soil Eh

Dissolved O_2 content of the floodwater was initially 7.8 ppm for

all temperature treatments (Fig. 6-1A). An inverse relationship

occurred between temperature and oxygen content over time. Oxygen

content decreased most rapidly and was lowest for the 22.5° and 30° C

treatments, whereas the 15° C treatment consistently had the highest

oxygen content. Floodwater oxygen contents had stabilized by day 10,

with 1.1, 2.1, and 3.3 ppm O_2 in the 30, 22.5, and 15° C treatments,

respectively.

For all treatments, soil Eh prior to submergence was approximately

+450 mv (Fig. 6-1B). As with floodwater oxygen content, an inverse

relationship generally exisited between temperature and soil Eh. By day

10, Eh of the 30°, 22.5°, and 15° C treatments was -14, +12, and +240

mv, respectively. By day 13, the soils of all treatments were anaerobic

(< 200 mv) (Ponnamperuma, 1972); however, Eh of the 30 and 22.5° C

treatments was near -30 mv, whereas that of the 15° C treatment was +160

mv.

For all treatments, soil pH increased during flooding, but more so

for the 22.5 and 30° C treatments than for the 15° C treatment. After

13 days of flooding, soil pH was 6.8, 6.7, and 6.4 for the 30°, 22.5°, and 15° C treatments, respectively.

Lenticel Morphology and Anatomy

Nonhypertrophic lenticels of mango are longitudinally oriented and characterized by a relatively loosely structured, nonsuberized filling tissue alternating with compact layers of thicker-walled, more highly suberized cells (Figs. 6-2 - 6-5). The phellogen of nonhypertrophied lenticels undergoes periclinal divisions to produce radially arranged rows of cells in the phellem and phelloderm (Figs. 6-2 - 6-5).

For plants maintained at 30° and 22.5° C, lenticel hypertrophy was first observed in a few plants on the fifth and sixth days of flooding, respectively. However, the mean number of days of flooding that elapsed until lenticel hypertrophy was observed was 6.6 ± 0.8 and 8.1 ± 0.7 (mean no. of days for 12 trees ± S.E.), for the 30° and 22.5° C treatments, respectively. Lenticel hypertrophy was not observed after 28 days of flooding at 15° C. However, plants transferred to the 30° C treatment after 28 days at 15° C exhibited lenticel hypertrophy within three days.

For plants flooded at 30° C and 22.5°, the development of hypertrophic lenticels (number per cm^2 of stem) followed a sigmoid pattern (Fig. 6-6) defined by the Gompertz Logistical Growth Model (Clow and Urquhart, 1974). Lenticel hypertrophy developed more rapidly at 30° C than at 22.5° C, as indicated by the steeper logarithmic growth phase of the 30° C regression line between days 5 and 10. For the 30° C treatment, virtually all stem lenticels at the floodline were

hypertrophied by day 10. Consequently, there was a reduction in the rate of development of lenticel hypertrophy after day 10 for the 30° C treatment. Thirteen days after flooding was initiated for the 30° C treatment, adjacent hypertrophic lenticels were coalescing due to pronounced hypertrophy. Although only about two-thirds of the lenticels had hypertrophied by day 10 for the 22.5° C treatment (Fig. 6-6), the rate of hypertrophy also appeared to be slightly decreasing for this treatment by day 13 of submergence.

Figures 6-7 through 6-10 and Figs. 6-11 through 6-12 show the development of lenticel hypertrophy for plants maintained at 22.5° and 30° C, respectively. Although there was no unaided visual evidence of hypertrophy until 5 days after submergence at 30° C, some histological changes preceeding hypertrophy were evident by day 3. Initial stages of lenticel hypertrophy were characterized by a more spherical shape of cells in the phellem and phelloderm (Figs. 6-8, 6-12), and by the development of intercellular spaces in the phellem and lenticel filling tissue (Fig. 6-12). As there was no evidence of tearing or mechanical disruption of the tissues, development of intercellular spaces was not considered to be an artifact of the sectioning procedure.

Later stages of hypertrophy were characterized by an increase in phellogen activity and production of additional phellem tissue adjacent to the lenticel pore, resulting in a larger pore opening (Figs. 6-9, 6-13). By day 6 of flooding, the increase in phellogen activity had produced a phellem layer with a mean thickness of 94.6 ± 8.7 μm and 76.9 ± 6.9 μm for the 30° C and 22.5° C treatments, respectively (mean phellem layer thickness of three representative sections from each of three trees per treatment ± S.E.). In contrast, nonhypertrophic

lenticels had a mean phellem layer thickness of 48.4 ± 7.1 μm (mean phellem layer thickness of three representative sections from each of three trees ± S.E.). Later stages of lenticel hypertrophy were also characterized by the development of intercellular spaces in the cortex (Fig. 6-14).

No effect of bark excision on hypertrophy or tree survival was observed.

Discussion

The decreased solubility of oxygen in water with increasing temperature, and increased microbial and root respiration apparently resulted in rapid oxygen depletion and rapid reduction of soil Eh at 30° and 22.5° C. The higher Eh and greater floodwater oxygen content of the 15° C treatment indicate reduced O_2 consumption at this temperature, and decreased root O_2 demand may have slowed the development of hypertrophic lenticels in these trees. The higher Eh and oxygen content, and the absence of lenticel hypertrophy at 15° C also suggest a critical floodwater oxygen content (3 ppm) above which lenticel hypertrophy in mango may be delayed or inhibited.

Development of intercellular spaces in adventitious roots of Zea mays was stimulated by low partial pressures of O_2 (Drew et al., 1979; McPherson, 1939). However, Jackson et al. (1985) reported that development of intercellular spaces in adventitious roots of Oryza sativa was not promoted by an O_2 deficit. Similarly, Wample and Reid (1975) reported that flooding with either stagnant or aerated water induced stem hypertrophy in Helianthus annuus. In previous experiments

with mango at temperatures of 25-30° C, lenticel hypertrophy was
inhibited by floodwater oxygen contents of 12-15 ppm, but no inhibition
was noted at a relatively low range of O_2 contents (1-5 ppm) similar to
those in the present study (K.D. Larson, unpublished data), suggesting
an oxygen effect on lenticel hypertrophy.

The increased phellogen activity and more rapid hypertrophy that
were observed at 30° C for mango may reflect the tropical and
subtropical origin of this species (Mukherjee, 1985). Hypertrophy is a
growth process involving phellogen activity, cell enlargement, and cell
elongation (Angeles, 1990; Kawase, 1981). Since cell division and
growth involve temperature-dependent enzymatic reactions and metabolic
processes, acceleration of lenticel hypertrophy with increasing
temperatures would be expected. McPherson (1939) reported that high
temperatures increased the development of intercellular space in flooded
roots of Zea mays. Similarly, for the temperate-zone species Fraxinus
pennsylvanica, phellogen activity increased with each 5° C increase in
temperature over a range of 10 to 30° C (Borger and Kozlowski, 1972).
However, phellogen activity of two other temperate-zone species, Robinia
pseudacacia and Ailanthus altissima, generally increased as temperature
increased up to 25° C, but decreased at 30° C (Borger and Kozlowski,
1972). Borger and Kozlowski (1972) also reported that periderm tissue
developed in F. pennsylvanica seedlings grown at at 10° C, but did not
develop in A. ailanthus, again indicating differences among species in
phellogen activity and periderm development in response to temperature.

Flood-induced anaerobiosis stimulates ethylene production in some
plants (Drew et al., 1979; Wample and Reid, 1975), and an ethylene-
mediated increase in cellulase activity is a prelude to hypertrophy or

development of aerenchymatous tissue (Kawase, 1981). Ethylene
production is temperature-dependent, with the optimum temperature for
ethylene evolution at about 30° C (Yang, 1980). Thus, with mango, the
more rapid hypertrophy observed at 30° than at 22.5° C, and the
inhibition of hypertrophy at 15° C, may be due, in part, to temperature
effects on ethylene biosynthesis.

The development of hypertrophic lenticels may have aided tree
survival at 22.5° and 30° C. At 15° C, phellogen activity and cell
growth of mango were reduced and lenticel hypertrophy did not occur,
although hypertrophy occurred rapidly when the trees were transferred to
30° C. At 15° C, soil and plant respiration and flooding stress
presumably were reduced, and lenticel hypertrophy was inhibited, but at
higher temperatures, O_2 consumption and plant stress increased, and
lenticel hypertrophy developed.

Conclusions

Although inhibition of lenticel hypertrophy in mango previously
was observed with floodwater oxygen contents of 12-15 ppm (K.D. Larson,
unpublished data), the small differences in floodwater O_2 content among
treatments in the present study suggest that differences in hypertrophy
probably were due to temperature rather than O_2 effects. Also, although
there was little difference in O_2 content and Eh between the 22.5° and
30° C treatments, development of hypertrophied lenticels was slower at
22.5° C. This also suggests a response to temperature rather than to
oxygen. Thus, inhibition of lenticel hypertrophy at 15° C appears to be
due mainly to temperature-mediated reductions in respiration and plant

metabolic processes that regulate phellogen activity and cell growth. Although various endogenous and exogenous factors (O_2 partial pressure, ethylene) may influence hypertrophy of lenticels, lenticel hypertrophy in mango appears to be a temperature-dependent response to flooding.

Fig. 6-1. Effect of floodwater temperature and flooding duration on floodwater dissolved O_2 content and soil pH. A) Floodwater dissolved oxygen content. B) Soil redox potential (Eh). Values represent means of 6 replicates per treatment. Different letters denote significant differences between treatments (Duncan's Multiple Range Test, $P < 0.05$). Absence of letters indicates no significance.
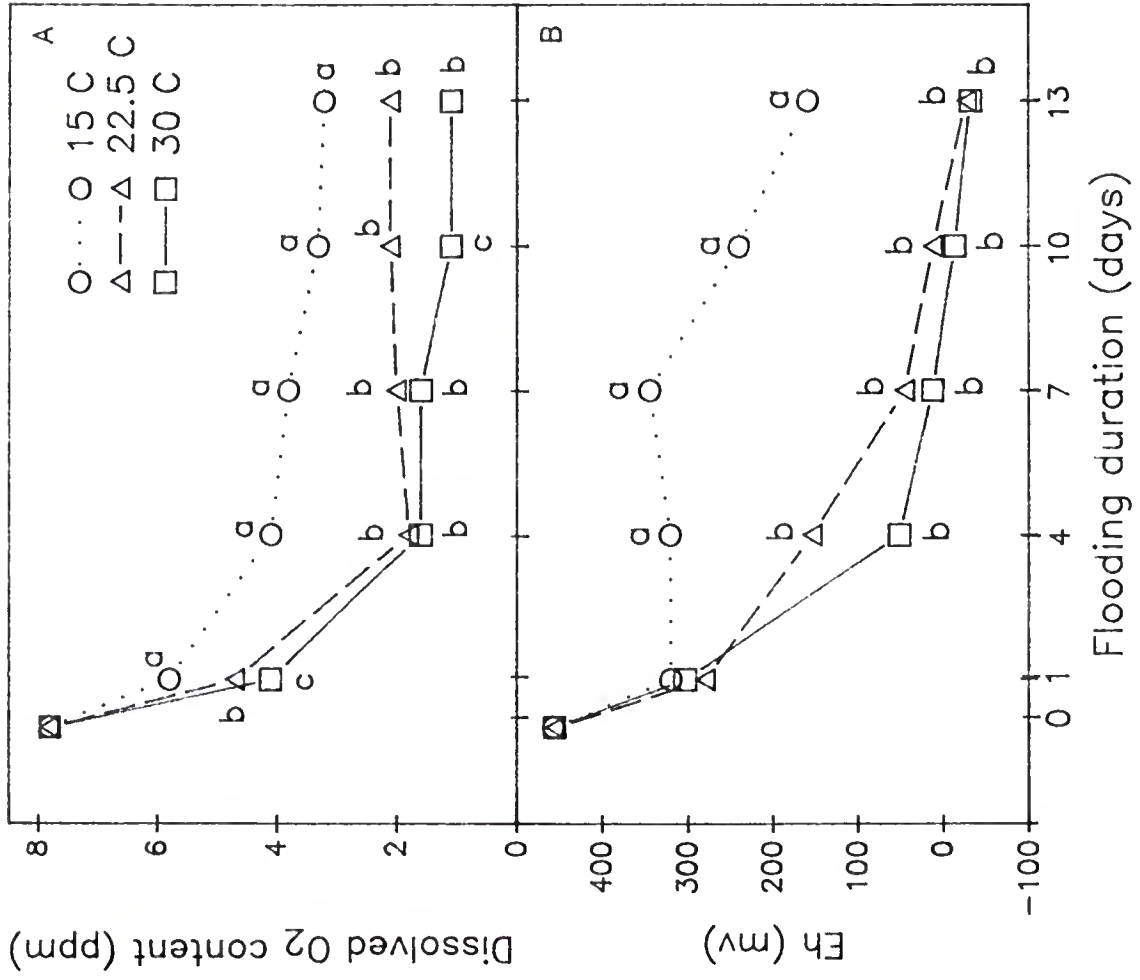
Figs. 6-2, 6-3. Non-hypertrophic stem lenticels of mango trees flooded at 15° C. Photographs are representative of ten sections from each of three trees; PH = phellem; PG = phellogen; PD = phelloderm; C = cortex. 6-2) Lenticel prior to flooding; 6-3) lenticel after 3 days of flooding.
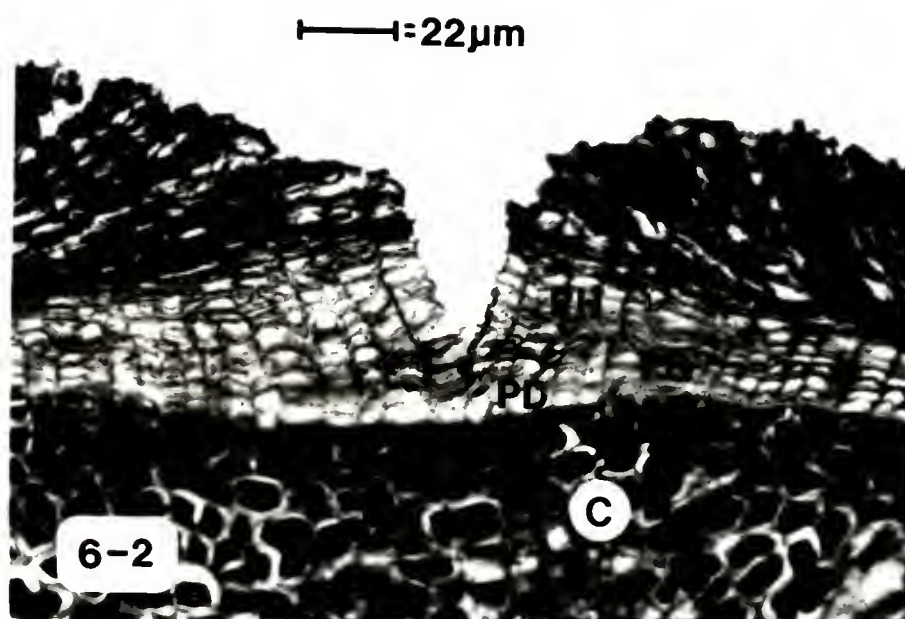
Figs. 6-4, 6-5. Non-hypertrophic stem lenticels of mango trees
    flooded at 15° C. Photographs are representative of ten
    sections from each of three trees; PH = phellem; PG =
    phellogen; PD = phelloderm; C = cortex. 6-4) lenticel after
    6 days of flooding; 6-5) lenticel after 12 days of flooding.
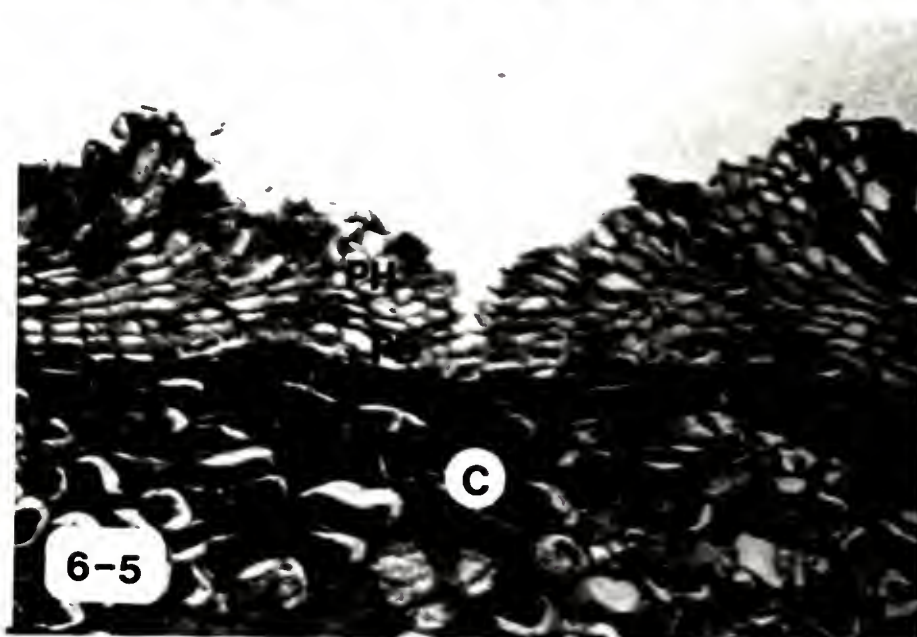   For scale, see Fig. 6-2.

6-4

6-5

Figure 6-6. Hypertrophic stem lenticel density as a function of floodwater temperature and flooding duration. Symbols represent mean number of hypertrophic lenticels ± SE in a randomly selected, 1-cm^2 area of tree stem at the floodline of each of 12 trees for each temperature treatment. Non-linear regression equations (Gompertz Logistical Growth Model, P < 0.01) were:

$$y = 10.74e^{-61.0e^{-0.68x}} \quad ; \quad r^2 = 0.68, \text{ and}$$

$$y = 11.4e^{-14.4e^{-0.33x}} \quad ; \quad r^2 = 0.62,$$

for the 30° C and 22.5° C treatments, respectively.
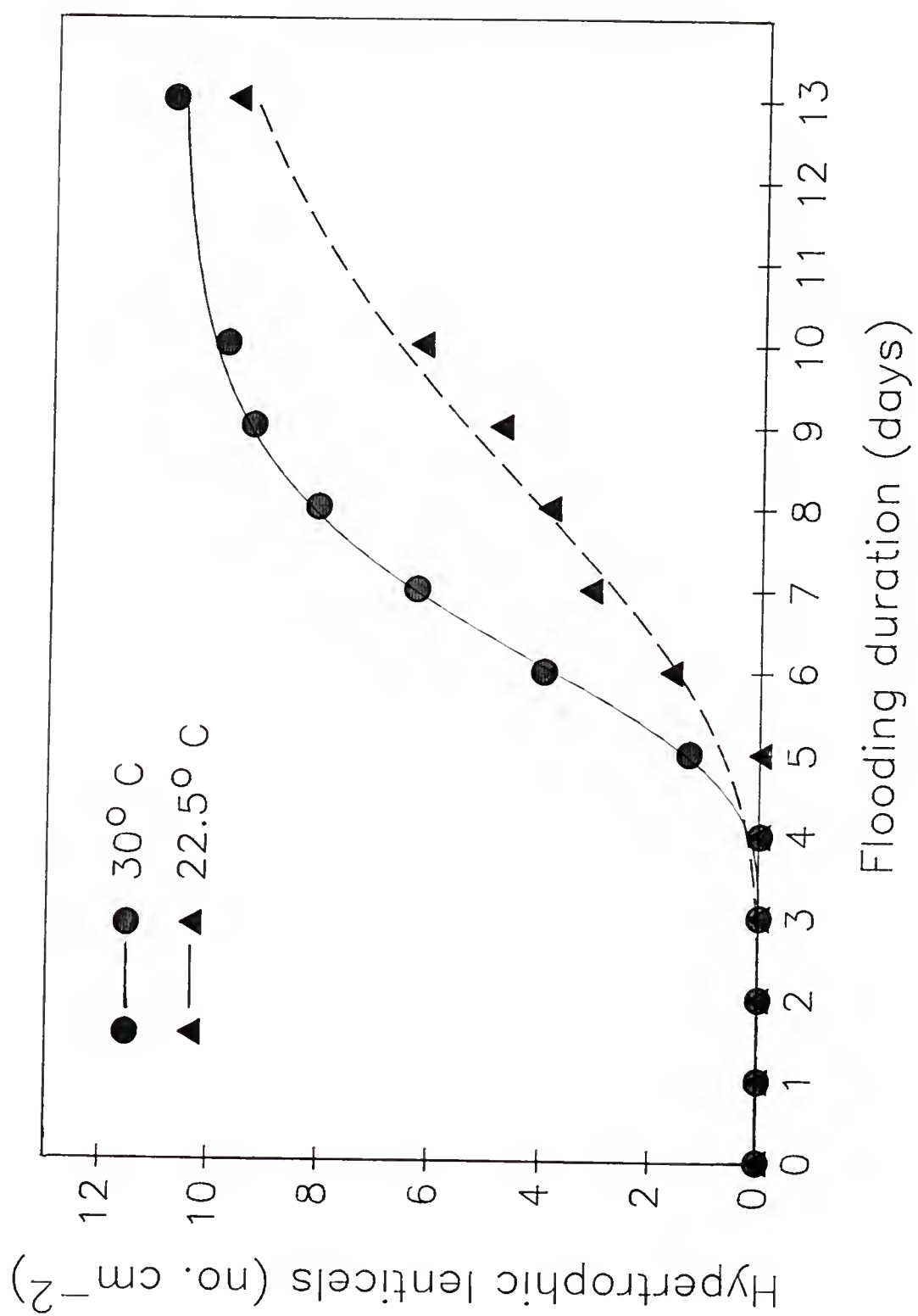
Figs. 6-7, 6-8. Development of stem lenticel hypertrophy in mango
    trees flooded at 22.5° C. Photomicrographs are representative
    of ten sections from each of three trees; PH = phellem; PG =
    phellogen; PD= phelloderm; C = cortex. 6-7) Non-hypertrophic
    lenticel prior to flooding; 6-8) Lenticel after 3 days of
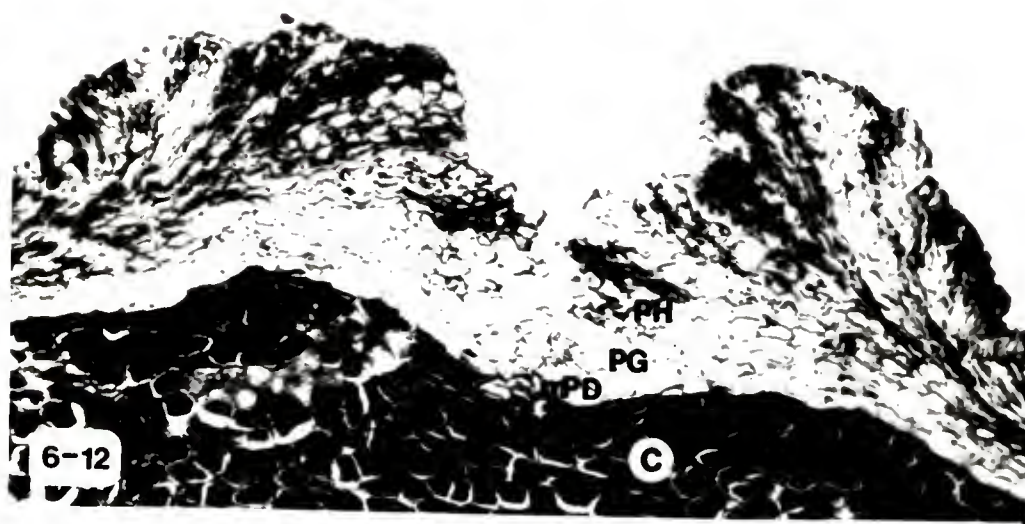   flooding.
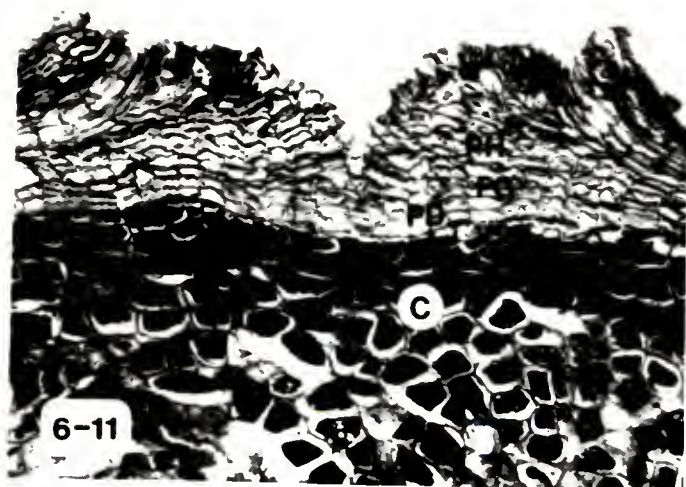
6-7

6-8
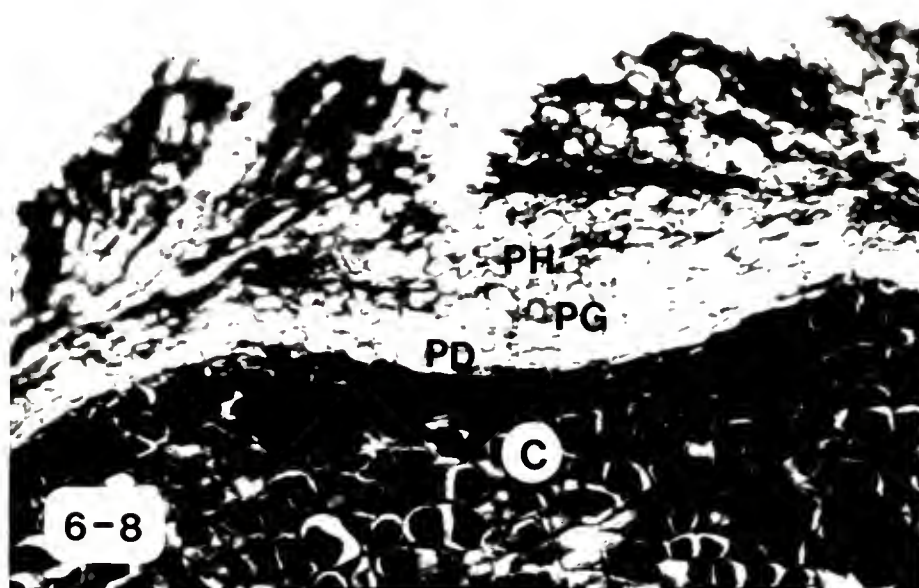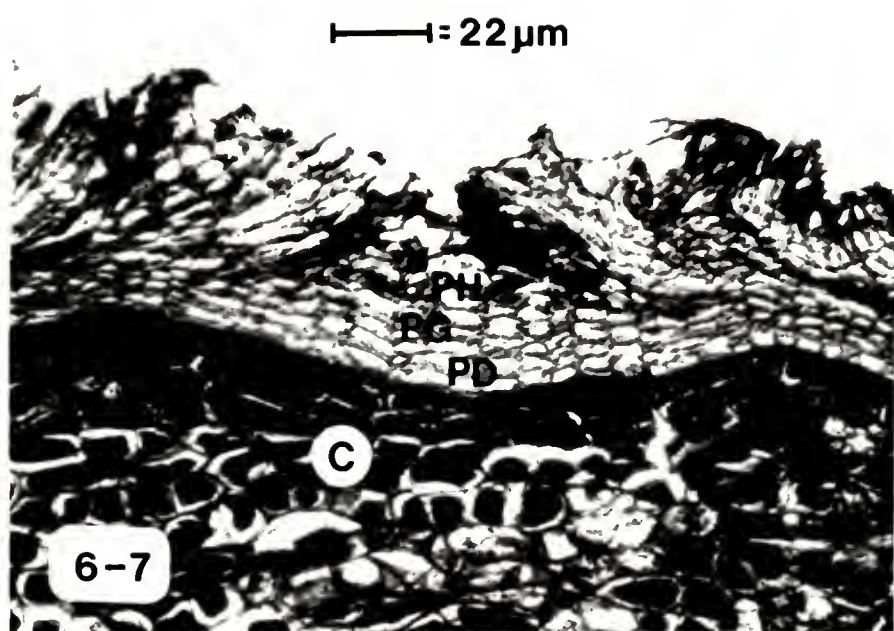
Figs. 6-9, 6-10. Development of stem lenticel hypertrophy in mango
trees flooded at 22.5° C. Photomicrographs are representative
of ten sections from each of three trees; PH = phellem; PG =
phellogen; PD= phelloderm; C = cortex. 6-9) Lenticel after 6
days of flooding; note increased production of phellem tissue;
6-10) Lenticel after 12 days of flooding. For scale, see Fig.
6-9.
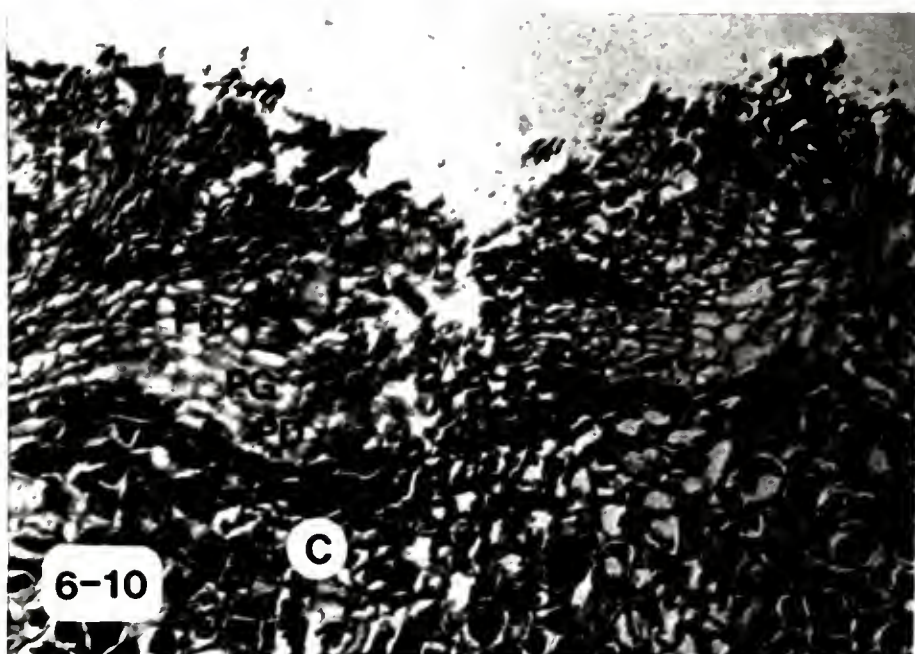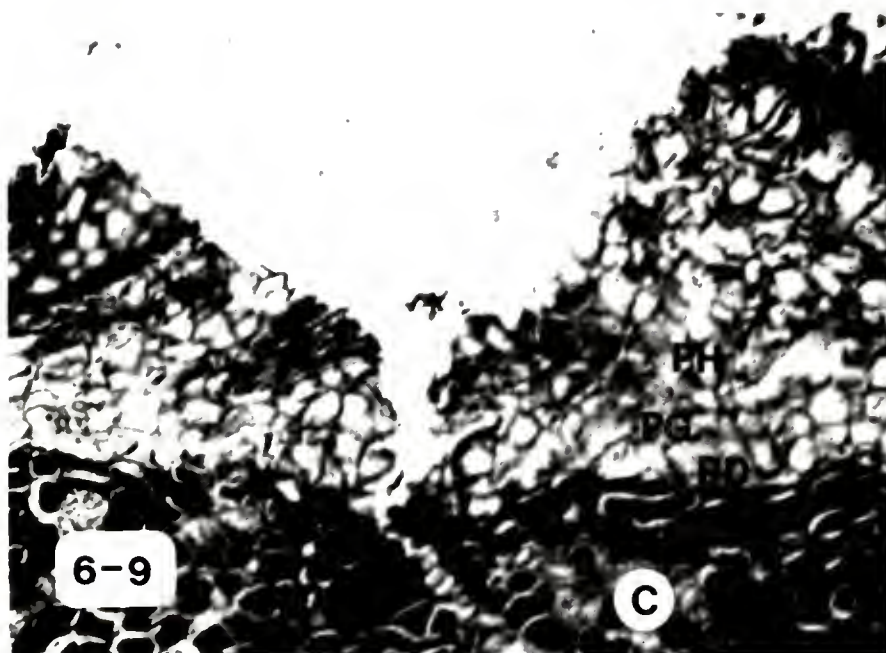
Figs. 6-11, 6-12. Development of stem lenticel hypertrophy in mango
trees flooded at 30° C. Photomicrographs are representative
of ten sections from each of three trees; PH = phellem; PG =
phellogen; PD = phelloderm; C = cortex. 6-11) Non-hypertrophic
lenticel prior to flooding; 6-12) Lenticel after 3 days of
flooding; note increased production of phellem tissue in area
adjacent to the lenticel.

6-11

6-12

Figs. 6-13, 6-14. Development of stem lenticel hypertrophy in mango trees flooded at 30° C. Photomicrographs are representative of ten sections from each of three trees; PH = phellem; PG = phellogen; PD = phelloderm; C = cortex. 6-13) Lenticel after 6 days of flooding; note increased production of phellem tissue; 6-14) Lenticel after 12 days of flooding. For scale, see Fig. 6-11.

6-13

6-14
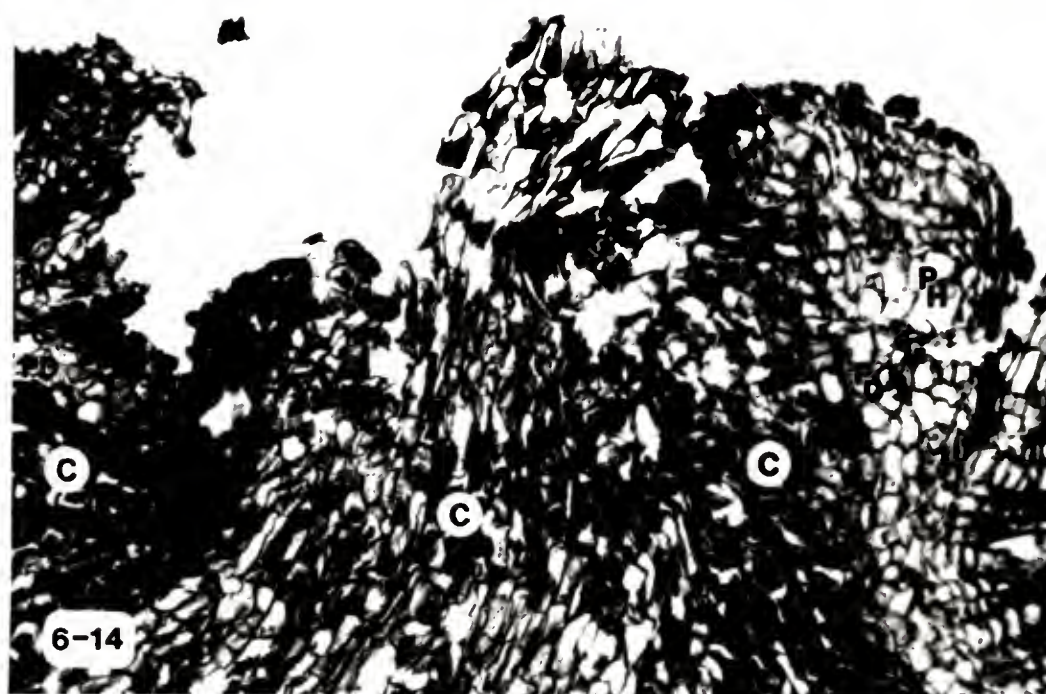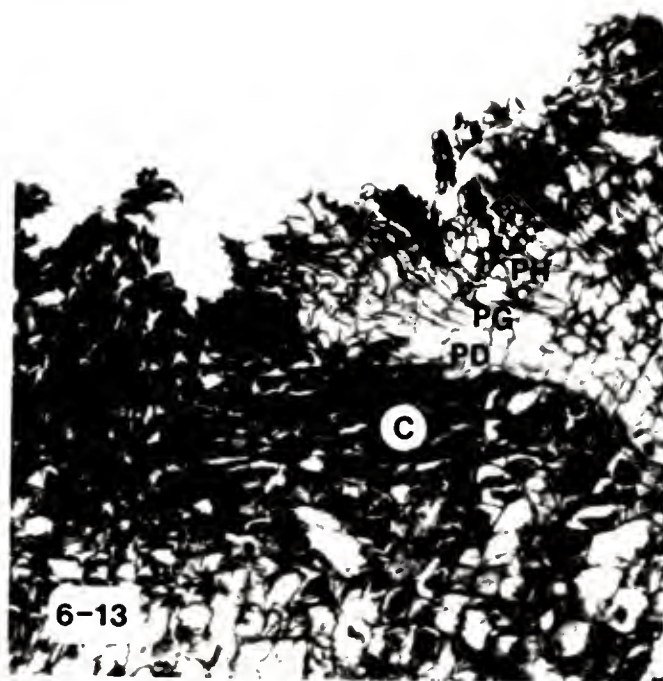
CHAPTER 7
FLOODWATER OXYGEN CONTENT, ETHYLENE PRODUCTION AND
LENTICEL HYPERTROPHY IN FLOODED MANGO TREES

Introduction

A common morphological response of plants to flooding is increased

intercellular space in roots and stems, such as the development of

aerenchyma, or stem and lenticel hypertrophy (Kawase, 1981). Low O_2 in

the rhizosphere, due to flooding, resulted in increased intercellular

space in the tissues of a number of plant species (Benjamin and

Greenway, 1979; Drew et al., 1979; McPherson, 1939; Topa and McLeod,

1986; Troughton, 1972). However, in a few species, flooding had no

effect on the amount of intercellular space (Jackson et al., 1985;

Wample and Reid, 1975). In previous experiments conducted with mango,

an inhibition of stem lenticel hypertrophy was observed with floodwater

oxygen contents of 12-15 ppm, but not at 1-5 ppm (see page 83, Chapter

6).

Flooding resulted in increased ethylene evolution in many plant

species (Bradford and Dilley, 1978; Drew et al., 1979; El-Beltagy and

Hall, 1974; Jackson and Campbell, 1975, 1976; Jackson et al., 1978;

Kawase, 1972, 1974, 1976, 1978; Wample and Reid, 1979). Ethylene

evolution from aerial plant parts is greater when roots are submerged in

water with low oxygen content compared to well-aerated water (Kawase,

1978). Ethylene can stimulate the development of intercellular space

and stem hypertrophy in nonflooded plants (Kawase, 1974), and in some flooded plants, inhibition of ethylene action inhibited aerenchyma formation (Drew et al., 1981). Thus, floodwater oxygen content may affect stem hypertrophy by affecting ethylene production.

The purpose of this study was to determine the relationship between dissolved oxygen in the floodwater, plant ethylene evolution and stem lenticel hypertrophy of flooded mango trees.

<div align="center">Materials and Methods</div>

Flooding Chambers

Clear flooding chambers were constructed that allowed manipulation of O_2 concentration in the floodwater and the withdrawal of small volumes of air adjacent to the tree stem (Fig. 7-1). Chambers consisted of 1-liter styrene-acrylonitrile containers fitted with removable, 9 cm x 14 cm x 0.5 cm (width x length x thickness) acrylic lids. A hole, slightly larger than the diameter of the tree stem, was made in the center of the lid and a slit (approximately 1.3 cm wide) was cut from the edge of the lid to the hole (Fig. 7-2). After the stem was slid into the hole in the lid, the slit was sealed by cementing a 1.3 cm strip of acrylic (Fig. 7-2a) into the slit. Adhesive, closed cell vinyl foam weatherstripping (3.18 cm wide x 0.5 cm thick) was wrapped around the stem and manually compressed to allow the lid to fit over it. With the lid in place, the weatherstripping expanded to form an airtight seal around the stem. In preliminary tests, vinyl foam weatherstripping did not produce ethylene or other volatile compounds under high temperature and irradiance conditions, typical of greenhouse conditions in this

study. Parafin, silicone sealants, glues, plasticine, and clay were also tried but either evolved ethylene or interfered with ethylene measurements.

Prior to placing the tree in the lid, a "collar" (Figs. 7-1a, 7-2b) was fitted around the stem to permit gas sampling from a relatively small volume of air surrounding the stem, thus minimizing the dilution of any volatile compounds produced by the tree. The collar was constructed by sliding acrylic tubing (9 cm long, 3.8 cm inner diameter, volume = 102 cm^3), over the leaves and around the base of the stem. The collar was then cemented to the underside of the lid.

The flooding chamber was filled with tap water to 4.5 cm below the top, creating an air space of approximately 350 cm^3 in the top of the chamber, and an air space of 51 cm^3 in the collar (Fig. 7-1). Adhesive, closed cell vinyl foam weatherstripping (0.95 cm wide, 1.27 cm thick) was placed between the top of the chamber and the lid, and plants were sealed in the chamber by firmly attaching the lid to the bottom of the chamber with four large elastic bands. When the chamber was sealed, the apical portion of the tree was outside and the roots and basal portion of the tree stem (total height = about 17 cm) were inside the chamber (Fig. 7-1). To maintain floodwater at a constant depth, tapwater was added twice daily through an access hole in the lid (Fig. 7-1b). The volume of the tree stem within the air space in the collar was calculated for each tree, and averaged about 20 cm^3; thus, with the tree in the chamber the air space in the collar was approximately 30 cm^3.

A standard aquarium pump (Fig. 7-3a) circulated air through four collars in four chambers at 0.65 liters min^{-1} $collar^{-1}$, via inlet (Fig.

7-1c, 7-3b) and outlet (Figs. 7-1d, 7-3c) tubes (tygon, 0.5 cm inner diameter) inserted through holes in the lids and collars.

Regulation of Floodwater Dissolved Oxygen Content

Pure N_2, ambient air, or pure O_2 gas were bubbled into the floodwater of different chambers to maintain floodwater dissolved O_2 contents of 1-2 ppm, 5-7 ppm, or 13-15 ppm, respectively. A control treatment had no gas bubbled into the floodwater, and also had a dissolved O_2 content of 1-2 ppm. There were thus four floodwater O_2 contents: 1) 1-2 ppm O_2 (using N_2 gas, achieving rapid anaerobiosis), 2) 1-2 ppm O_2 (using stagnant water with no bubbling, achieving slow anaerobiosis), 3) 5-7 ppm O_2 (using ambient air), and 4) 13-15 ppm O_2 (using O_2 gas). These four O_2 contents are referred to as the 1-2 ppm (rapid), 1-2 ppm (slow), 5-7 ppm, and 13-15 ppm O_2 treatments, respectively. For the 5-7 ppm treatment, the ambient air was passed through a 2-liter flask containing soda lime to remove CO_2.

Gases flowed from pressurized cylinders of pure O_2 and N_2 (Fig. 7-3d), or, in the case of the ambient air, from a 0.124 kilowatt air pump (Model 4870, Emerson Corp., St. Louis, MO), through tygon tubing (1.0 cm inner diameter) to manifolds (Fig. 7-3e) constructed of 3 cm diameter polyvinyl chloride tubing. Gas flows were regulated by timeclock-controlled solenoid valves (Fig. 7-3f). Gas from the manifold flowed into the floodwater through 0.5 cm (inner diameter) tygon tube (Fig. 7-3g) inserted through a hole in the lid. The end of the tubing was fitted with a silica aquarium stone (2.54 cm in length) (Figs. 7-1e, 7-3h). A similar tube inserted through the lid served as the exhaust port for the gas (Figs. 7-1e, 7-3i). The specified floodwater dissolved

oxygen contents in the chambers were maintained by adjusting the duration and timing of gas flow. There were 3 manifolds, one for each pressurized gas (N_2, O_2 or ambient air), with three flooding chambers attached to each manifold. A fourth chamber was not connected to the manifold, and was maintained as the 1-2 ppm (slow) treatment. There were 3 individual tree replicates for each of the 4 floodwater oxygen levels.

For each chamber, dissolved O_2 content of the floodwater was monitored 2-4 times a day with a dissolved oxygen meter (Model 5946-55, Cole-Parmer Co., Chicago, Illinois) inserted through the access hole in the lid (Fig. 7-1b).

Stem Lenticel Hypertrophy

Seedling 'Peach' mango trees were grown outdoors in 3.75-liter pots in sand for 1.5 - 2 years. The trees were trained to a central leader and pruned periodically to maintain tree height at about 0.75 m. Mean tree stem diameter at a height 10 cm above the soil surface was about 1.5 cm.

The roots of twelve uniform trees were carefully removed from the sand, gently washed, and the trees placed in the individual flooding chambers in a greenhouse as described above. Trees were flooded for 2 weeks, and the number of hypertrophic stem lenticels were counted daily for each tree. Lenticels were considered hypertrophic if white parenchymatous tissue was detected in the lenticel pore during visual examination. The experiment was repeated twice, and there was no difference in the rate of hypertrophy for a given oxygen treatment ($P > 0.05$) among the three experiments. Therefore, experiments were combined

and mean stem lenticel hypertrophy calculated for the 9 trees in each oxygen treatment. Floodwater temperatures averaged 24° C, and temperature and relative humidity in the greenhouse ranged between 20° and 32° C, and 42-85%, respectively, during the experimental flooding periods.

Ethylene Evolution

Twelve trees, similar to those described for the lenticel hypertrophy experiment, were placed in the individual flooding chambers as previously described. Temperature and relative humidity in the greenhouse were similar to those described for the lenticel hypertrophy experiments.

Ethylene evolution from the stems of all plants in each treatment was determined daily. The inlet and outlet tubes of the stem collars (Figs. 7-1b, 7-1c) were sealed with rubber septae for 4 hrs to permit accumulation of ethylene in the enclosure. The pressurized gases tended to displace the water in the stem collars when the inlet and outlet tubes were sealed, thereby increasing the volume of the airspace in the collar. It was therefore necessary to shut off the flow of gases into the chambers during this 4-hr interval. For each plant, 1 cm^3 of air was removed from the collar with a 1 cm^3 gas-tight syringe inserted through the septae. The gas samples were analyzed for ethylene concentration using a gas chromatograph (Varian Model 3700), equipped with a 2 m X 3 mm stainless steel, 60/80 mesh alumina column and a flame ionization detector (Nunez-Elisea and Davenport, 1986). Ethylene was analyzed within 20 min of sampling. The experiment was repeated, and there was no difference in ethylene evolution (nL g^{-1} stem hr^{-1}, P >

0.05) between the two experiments for a given aeration treatment. Therefore, experiments were combined and mean ethylene evolution determined for the 6 trees in each oxygen treatment.

Results

Stem Lenticel Hypertrophy

For the 1-2 ppm (rapid) and the 1-2 ppm (slow) treatments, the dissolved oxygen content of the floodwaters was 1-2 ppm for most of the 2-week flooding period. This O_2 content was not, however, achieved until after about 12-18 hrs for the rapid treatment, and not until after 48 hrs for the slow treatment (data not shown).

Lenticel hypertrophy was first observed on the fifth day of flooding in some of the plants in the 1-2 ppm (rapid), 1-2 ppm (slow), and 5-7 ppm treatments, but hypertrophy did not develop before the sixth day of flooding for the 13-15 ppm treatment. However, the mean (± S.E.) number of days of flooding that elapsed until hypertrophy was first observed was 5.9 ± 0.3, 6.1 ± 0.3, 6.7 ± 0.6, and 9.2 ± 0.8 for the 5-7 ppm, 1-2 ppm (rapid), 1-2 ppm (slow), and 13-15 ppm treatments, respectively.

For all treatments, the development of lenticel hypertrophy (number per tree) followed a sigmoidal growth pattern (Fig. 7-4) defined by the Gompertz Logistical Growth Model (Clow and Urquhart, 1974). For plants in the 1-2 ppm (rapid), 1-2 ppm (slow), and 5-7 ppm treatments, there was no statistical interaction between flooding duration and floodwater oxygen content (P > 0.05) with regard to the number of hypertrophied lenticels. Therefore, plants from these three treatments

were pooled to analyze the time required for lenticels to hypertrophy.

Lenticel hypertrophy was more rapid for plants in the 1-2 ppm and 5-7

ppm treatments than for plants in the 13-15 ppm treatment, as indicated

by the steeper exponential growth phase of the regression line for

plants in these treatments compared to the 13-15 ppm treatment. For the

1-2 ppm (rapid and slow) and 5-7 ppm treatments, nearly all lenticels at

the floodline had hypertrophied by day 12 of the experiment.

Consequently, there was a reduction in the rate of hypertrophy after day

12 for these treatments. The number of hypertrophied lenticels in

plants in the 13-15 ppm treatment was less than half that of plants in

the other treatments by the end of the experiment, however, it is

unclear whether the rate of hypertrophy was decreasing for the 13-15 ppm

treatment at that time.

Ethylene Evolution

At day 0, ethylene evolution was about 0.5 nL g^{-1} stem hr^{-1} for

plants in all treatments (Fig. 7-5). There was little variation in

ethylene evolution for plants in the 13-15 ppm treatment over the course

of the experiment. After only one day of flooding, ethylene evolution

from plants in the control treatment was more than twice that of plants

in the other treatments. By day 2, ethylene evolution from plants in

the 1-2 ppm (slow) treatment was about three-fold greater than that from

plants in the 13-15 ppm treatment, and about 1.5-fold greater than that

of plants in the 1-2 ppm and 5-7 ppm treatments. For the 1-2 ppm (slow)

trees, ethylene evolution increased to about 0.4 nL g^{-1} stem hr^{-1} by day

4, and remained near 0.3-0.4 nL g^{-1} stem hr^{-1} during the remainder of

the experiment. During the first 5 days of flooding, ethylene evolution

from plants in the 1-2 ppm (rapid) treatment lagged behind that of the controls. However, by day 6, the plants in the 1-2 ppm (rapid) treatment produced the greatest amount of ethylene (about 0.45 nL g^{-1} stem hr^{-1}), and ethylene production from this treatment was generally greatest for the duration of the experiment. Although there was an increase in ethylene evolution from plants in the 5-7 ppm treatment on day 2 of flooding, ethylene production in plants in this treatment decreased to that of plants in the 13-15 ppm treatment over the next nine days of flooding, before increasing slightly toward the end of the experiment.

Discussion

The more rapid stem lenticel hypertrophy for mango trees exposed to 1-2 ppm O_2 or 5-7 ppm O_2 compared to trees exposed to 13-15 ppm O_2 floodwater indicates that lenticel hypertrophy is stimulated by low (1-7 ppm) partial pressures of O_2, and is not solely a hydration effect as suggested by Wample and Reid (1975). A similar promotion of lenticel hypertrophy, or of root or stem porosity, by low partial pressures of O_2 has been reported for various other species (Benjamin and Greenway, 1979; Drew et al., 1979; McPherson, 1939; Topa and McLeod, 1986; Troughton, 1972). In Helianthuus annuus, the development of stem hypertrophy was attributed to the presence of water in excess of field capacity, regardless of floodwater oxygen content (Wample and Reid, 1975). Wample and Reid (1975) continuously aerated the floodwater with compressed air, resulting in an 85% oxygen saturation of the floodwater. In our experiment, ambient air was bubbled into the floodwater resulted

in an approximate 65% oxygen saturation of the floodwater; bubbling pure oxygen into the floodwater resulted in an oxygen saturation of 100%, and it was only with pure oxygen that we were able to detect a reduction in the rate of lenticel hypertrophy.

Anaerobic flooding of other species has been reported to result in greater ethylene evolution than aerobic flooding (Kawase, 1978; Drew et al., 1979; Wample and Reid, 1979). A transient, but significant, increase in ethylene evolution occurred from the stems of trees in the 5-7 ppm treatment during the day 2 of flooding, but not from the trees in the 13-15 ppm treatment.

Flood-induced anaerobiosis can stimulate ethylene production in some plants (Drew et al., 1979; Wample and Reid, 1975), and an ethylene-mediated increase in cellulase activity is a prelude to hypertrophy or development of aerenchymatous tissue (Kawase, 1981). Thus, the rapid hypertrophy with floodwater O_2 contents of 1-7 ppm, and inhibition of hypertrophy with O_2 contents of 13-15 ppm, may be due to differences in ethylene production resulting from differences in floodwater O_2 content.

In quantifying ethylene evolution, it was necessary to stop the flow of pressurized gases into the chambers each day during the 4-hour period required for ethylene accumulation. This resulted in transient decreases in floodwater dissolved oxygen contents in the O_2 and aerated treatments during this period. For this reason, direct correlations between lenticel hypertrophy and stem ethylene evolution observed in the lenticel hypertrophy and ethylene evolution experiments could not be made. However, rates of lenticel hypertrophy and total number of hypertrophied lenticels noted were in general agreement in both experiments. The lack of an increase in ethylene evolution in the 13-15

ppm treatment, and the slower rate of hypertrophy for this treatment suggested that anaerobic stimulation of endogenous ethylene may have enhanced lenticel hypertrophy in mango.

Conclusions

For mango trees flooded at temperatures of 25-30° C, floodwater O_2 contents of 1-7 ppm generally resulted in hypertrophy of stem lenticels within about 6 days of flooding, whereas a floodwater O_2 content of 15 ppm delayed hypertrophy until about day 9. Similarly, after 14 days of flooding, there were more than twice the number of hypertrophied lenticels per tree with floodwater O_2 contents of 1-7 ppm than with floodwater O_2 contents of 15 ppm. Ethylene evolution from aerobic stem tissue increased 4- to 8-fold in trees exposed to floodwater O_2 contents of 1-2 ppm, increased 2-fold for trees exposed to floodwater O_2 contents of 6-7 ppm, but remained constant with floodwater O_2 contents of 13-15 ppm. These data suggest that ethylene plays a role in promotion of stem lenticel hypertrophy in flooded mango trees.

Fig. 7-1. Longitudinal view of a single flooding chamber used for studying the effect of floodwater dissolved oxygen content on stem lenticel hypertrophy and ethylene evolution from mango stem tissue. A) stem collar; B) access hole; C) inlet tube to stem collar; D) outlet tube from stem collar; E) aquarium stone at end of inlet tube leading from pressurized gas source; F) outlet tube for pressurized gas.
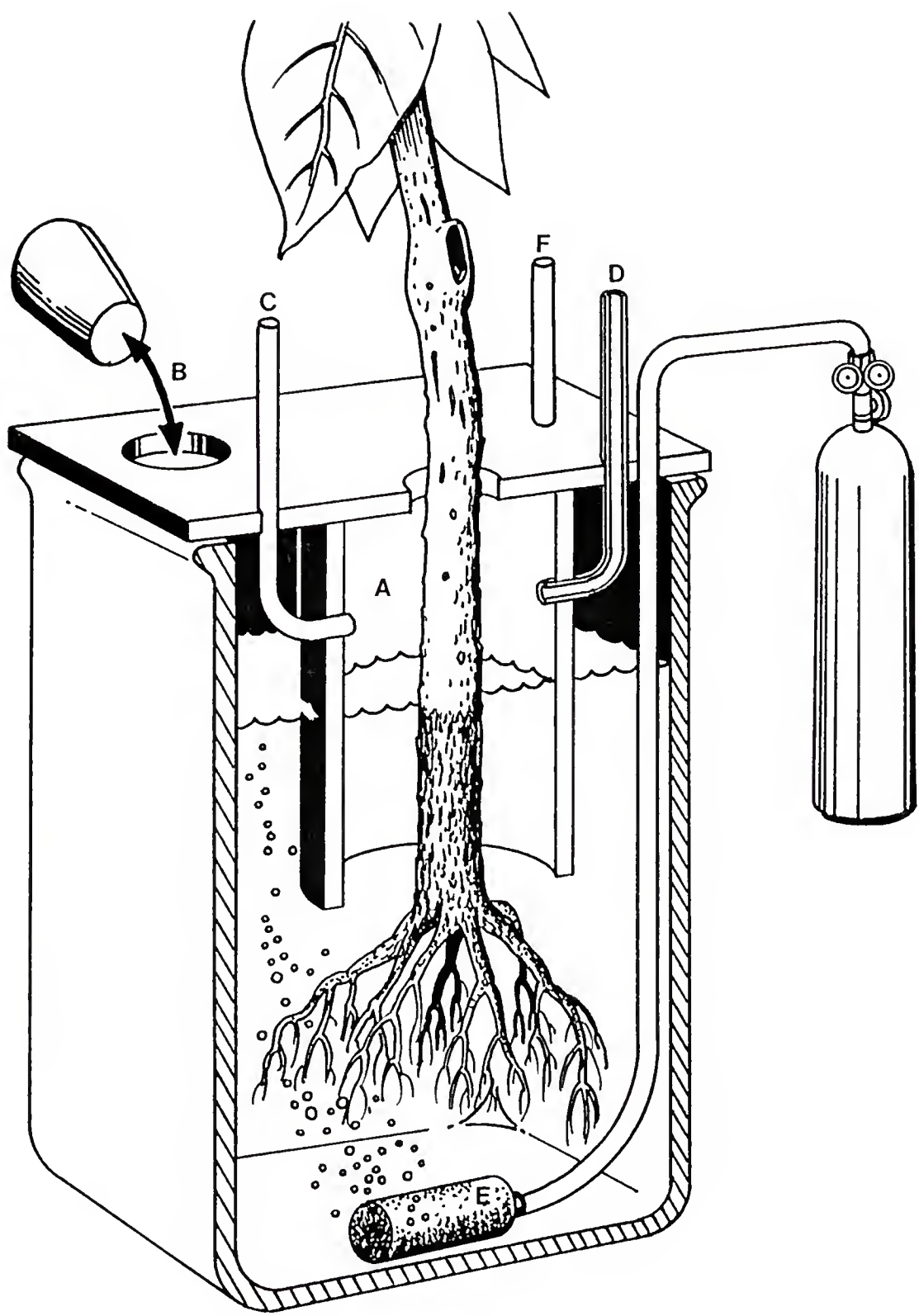
Fig. 7-2. Assembly of flooding chamber, showing placement of the tree in the stem collar and the in lid of the chamber. A) acrylic strip used to seal the slot in the lid; B) stem collar.
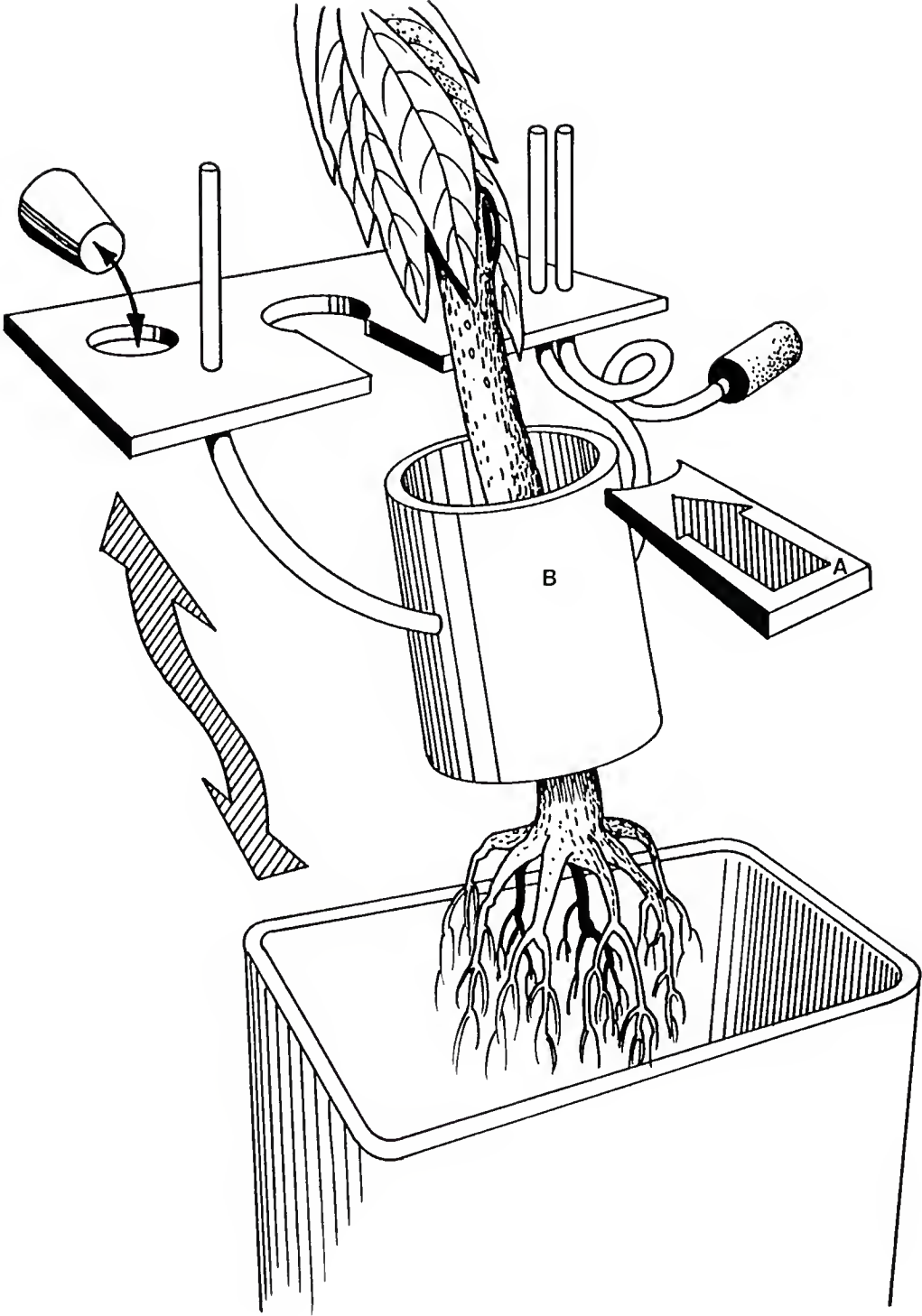
Fig. 7-3. Diagram of four flooding chambers. A) aquarium pump; B) inlet tube to stem collar; C) outlet tube from stem collar; D) pressurized gas cylinder; E) manifold; F) time-clock controlled solenoid valve; G) floodwater aeration tube; H) aquarium stone; I) outlet tube for pressurized gas.
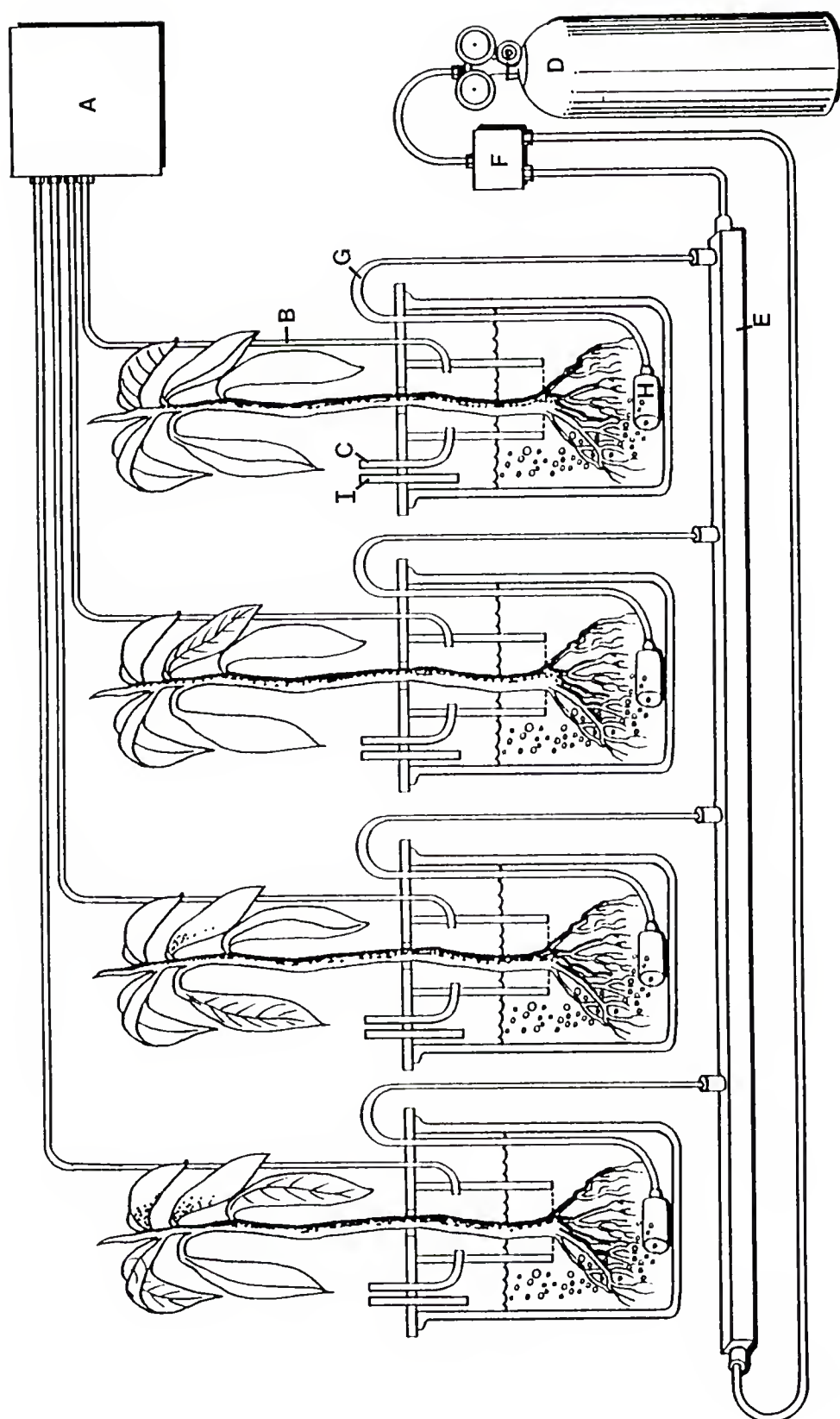
Fig. 7-4. Number of hypertrophic stem lenticels per mango tree (cv Peach) as a function of floodwater dissolved oxygen content and flooding duration. Symbols represent mean number of hypertrophic stem lenticels ± SE at or near the floodline for nine trees in each floodwater oxygen treatment. Floodwater O_2 contents of 13-15 ppm, 5-7 ppm, 1-2 ppm (rapid), and 1-2 ppm (slow) were achieved by bubbling pure O_2, ambient air, pure N_2, or no bubbling of any gas, respectively, into the floodwater in the chambers. For the 1-2 ppm treatments, "rapid" or "slow" indicates the rate of development of anaerobiosis. The 5-7 ppm, 1-2 ppm (rapid), and 1-2 ppm (slow) treatments were pooled since there were no statistical interactions between days of flooding and number of hypertrophied lenticels for these treatments. Non-linear regression equations (Gompertz Logistical Growth Model, P < 0.01) were:

$$y = 59.4e^{-62.5e^{-0.54x}} \quad ; \quad r^2 = 0.83, \text{ for the pooled treatments, and}$$

$$y = 21.5e^{-140.3e^{-0.55x}} \quad ; \quad r^2 = 0.55, \text{ for the 13-15 ppm treatment.}$$
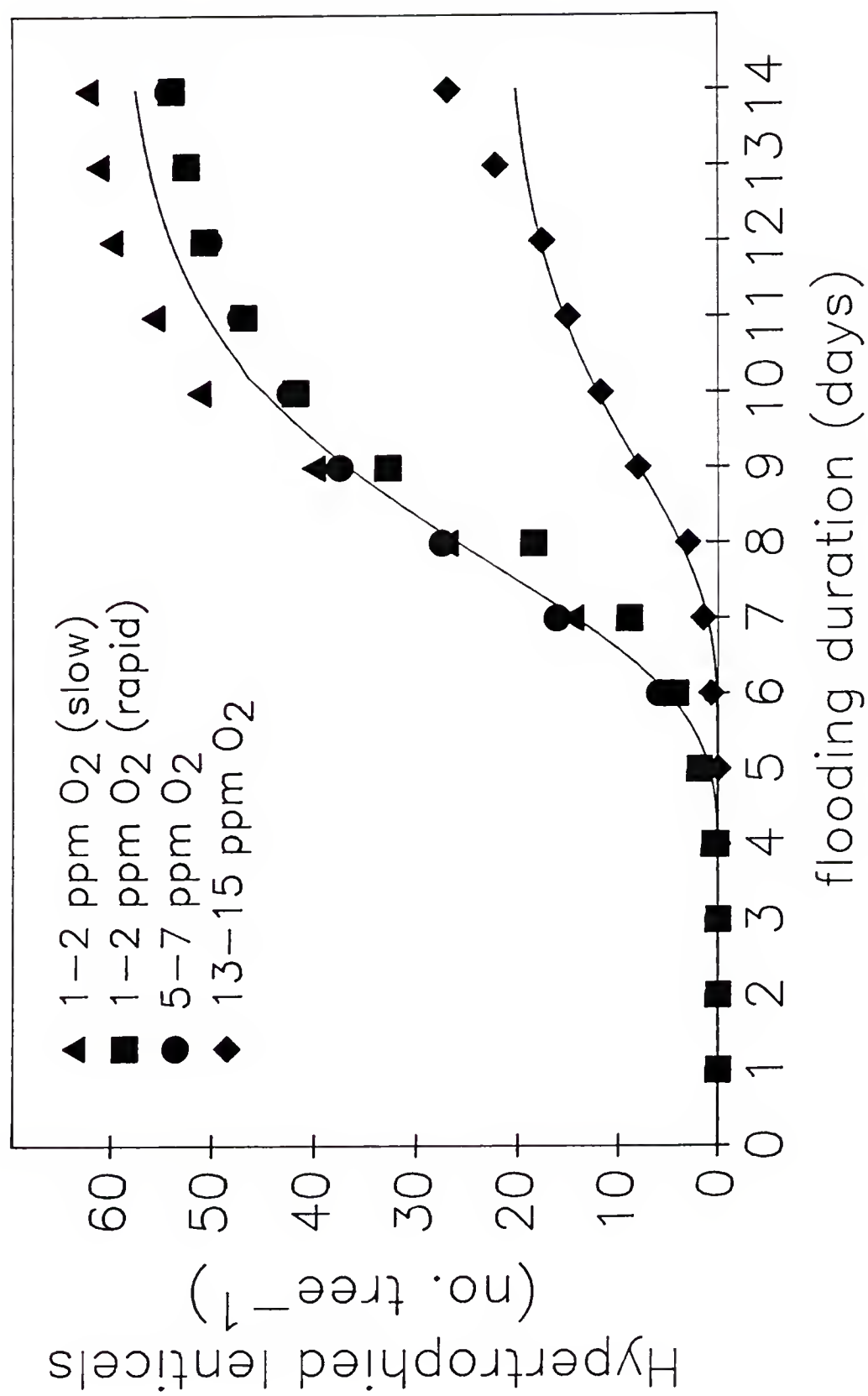
Fig. 7-5. Mean ethylene evolution from intact aerated stem tissue of flooded mango (cv Peach) trees as a function of floodwater dissolved oxygen content and flooding duration. Symbols represent means of six trees ± SE. Floodwater O_2 contents of 13-15 ppm, 5-7 ppm, 1-2 ppm (rapid), and 1-2 ppm (slow) were achieved by bubbling pure O_2, ambient air, pure N_2, or no bubbling of any gas, respectively, into the floodwater in the chambers. For the 1-2 ppm treatments, "rapid" or "slow" indicates the rate of development of anaerobiosis.
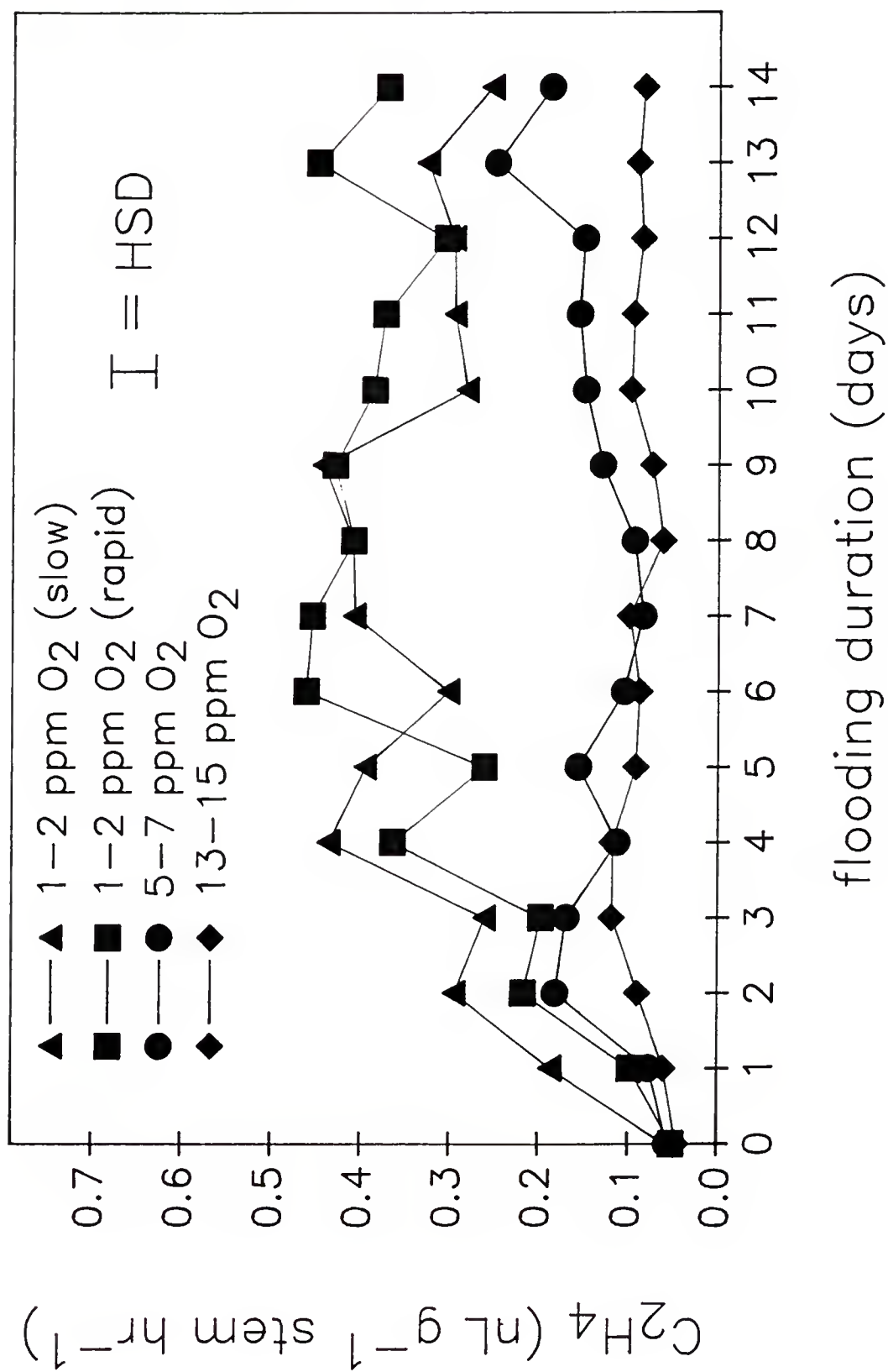
CHAPTER 8
CONCLUSIONS

Iron and manganese deficiencies frequently limit crop growth and productivity in South Florida limestone soils. However, upon flooding, significant chemical transformations occur in these soils, resulting in decreased soil pH and increased solubility of Mn and Fe in the soil solution. Although flooding reduces stomatal conductance and transpiration in mango trees, and results in increased root mortality, short-term flooding of these limestone soils can result in increased foliar iron and manganese concentrations in mango trees.

The concomitant increase in substomatal CO_2 concentration with reductions in A and g_s suggests that nonstomatal limitations to CO_2 assimilation may be greater than stomatal limitations. Reductions in leaf gas exchange in flooded mango occurred without reductions in leaf water potential.

Flood-induced mortality was noted in only one experiment, but mortality did not appear to be related to tree age, *per se*. In our experiments with containerized mango trees, young trees (aged 2 months to 2 years) never died as a result of short-term flooding, but older trees (aged 3 to 4 years) occassionally died. In these experiments, the shoots of the young trees were pruned on a regular basis to maintain trees at a manageable size, but shoots of the older trees were not pruned. The reduction in mango root growth with flooding, coupled with the larger shoot mass of the older trees, may have resulted in a

severely imbalanced root:shoot ratio in the older trees, resulting in tree death.

Under ambient conditions, hypertrophy of stem lenticels was observed in trees that survived flooding stress, but not in trees that died. Furthermore, when hypertrophied lenticels of flooded mango trees were covered, the trees died within three days, suggesting that, as in studies with other woody plants, hypertrophied lenticels allow internal oxygen diffusion to submerged roots, or excretion of potentially toxic byproducts of anaerobic respiration. Hypertrophy of stem lenticels was most rapid at floodwater temperatures of $30°$ C, slightly less rapid at temperatures of $22.5°$ C, and did not occur at $15°$ C. Thus, in mango, stem lenticel hypertrophy is a temperature-dependent growth process. Although hypertrophy did not occur at $15°$ C, these trees did not die, presumably because of the reduced respiration rates, and hence, reduced oxygen demand of the roots of plants in this treatment.

Anatomical studies revealed that hypertrophy is due, in part, to increased activity of the lenticel phellogen, and to increased intercellular space in the lenticel and subtending cortex. The phellogen undergoes periclinal division to produce phellem tissue, resulting in an enlargement of the lenticel and a widening of the lenticel pore. Flood-induced anaerobiosis can stimulate ethylene production in some plants, and an ethylene-mediated increase in cellulase activity hasbeen shown to be a prelude to stem hypertrophy or development of aerenchymatous tissue. The optimum temperature for ethylene evolution is $30°$ C. Thus, the more rapid hypertrophy observed at $30°$ C than at $22.5°$ C, and the inhibition of hypertrophy at $15°$ C, may be due to temperature effects on ethylene biosynthesis, although

other temperature-dependent metabolic processes (respiration, cell growth) are also probably involved.

At air temperatures between 20° and 32° C, and floodwater temperatures of 24° C, stem lenticel hypertrophy in mango was dependent on floodwater dissolved oxygen content. Floodwater oxygen contents of 13-15 ppm delayed, but did not completely inhibit hypertrophy, whereas floodwater dissolved oxygen contents of 1-7 ppm resulted in rapid and profuse hypertrophy.

With floodwater dissolved oxygen contents of 1-2 ppm, two- to three-fold increases in ethylene evolution were observed from intact mango stem tissue after only one day of flooding, and four- to eight-fold increases in ethylene evolution were observed over a two-week flooding period. Flooding mango trees in oxygenated (13-15 ppm O_2) floodwater had no detectable effect on ethylene evolution, but floodwater with 5-7 ppm O_2 resulted in intermediate, but variable, ethylene evolution.

Mango trees cannot be considered hydrophytic plants, since flooding results in reduced gas exchange and vegetative growth, and, occassionally, mortality. However, mango trees appear to possess certain adaptations to flooded soil conditions, such as hypertrophied lenticels and, in a small percentage of trees, adventitious roots. Also, mango trees continue nutrient uptake under flooded soil conditions, and may actually increase uptake of certain elements during flooding. Therefore, in South Florida and in areas with similar edaphic conditions, the possibilty exists to use short-term flooding as a management tool to increase the availability of certain minor elements to mango trees.

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BIOGRAPHICAL SKETCH

Kirk David Larson was born in Pasadena, California on July 1, 1953, the second of four children. He resided in Arizona, California, and New Jersey before moving to Puerto Rico in 1966. Following graduation from high school in 1971, he was employed on a farm in the southern part of Puerto Rico. Kirk worked on agricultural development projects in Guatemala and Venezuela from 1977 through 1980, and was awarded the B.S. degree in international agricultural development from the University of California, Davis in 1980. In 1984, he was awarded the M.S. degree in horticulture (pomology) from the University of California, Davis. Since 1971, Kirk has worked continuously in research, extension, or production of fruits, vegetables and agronomic crops. His research interests focus on production physiology, propagation and management of fruit crops, and low-input sustainable agriculture.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frederick S. Davies, Chair
Professor of Horticultural Science

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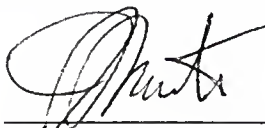
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This dissertation was presented to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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